THE GENERA OF PINACEAE IN THE SOUTHEASTERN UNITED STATES[1]

ROBERT A. PRICE[2]

PINACEAE Lindley, Nat. Syst. Bot. ed. 2. 313. 1836, nom. cons.

(PINE FAMILY)

Evergreen [or deciduous], monoecious trees (occasionally shrubs), usually pyramidal in form. Leaves linear to acicular [rarely lanceolate], spirally arranged (often apparently 2-ranked), sessile or short-petiolate; foliage leaves either borne on long-shoots or clustered tightly on short-shoots. Pollen cones (microsporangiate strobili) bearing spirally arranged, bilaterally symmetrical microsporophylls; microsporangia 2 on the abaxial surface of each sporophyll, longitudinally or transversely [or obliquely] dehiscent; pollen grains bisaccate, or less commonly with the saccae reduced to a frill (in *Tsuga* sect. TSUGA) [or nonsaccate in *Larix* and *Pseudotsuga*]; prothallial cells 2. Ovulate cones with

spirally arranged, strongly flattened bract-scale complexes; bracts included or exserted, separate from the scales for most of their length; mature ovuliferous scales relatively thin to strongly thickened and woody (in *Pinus*); ovules 2 on the adaxial surface of each scale, the micropyles directed toward the cone axis; archegonia few per ovule, not clustered. Seeds with an elongate terminal wing partially folded around the seed body [wing short or absent in some species of *Pinus*]; embryo straight, cotyledons 2–12[–18]. Chromosome number $2n = 24$ [26 and 44 in one species each]. (Including Abietaceae Walpers; Abietineae Rich.) TYPE GENUS: *Pinus* L.

The largest and most economically important family of conifers, with ten genera and approximately 220 species, the Pinaceae are restricted almost entirely to the Northern Hemisphere[3] both at present and as fossils (Florin, 1963). Three small genera are confined to eastern Asia: *Keteleeria* Carr., a genus of perhaps nine species (Cheng & Fu) much in need of further study, and the monotypic *Cathaya* Chun & Kuang (described in 1958 from southern China) and *Pseudolarix* Gordon (golden larch, false larch). *Cedrus* Trew, comprising the true cedars, consists of four closely related species occurring disjunctly in North Africa, the Near East, Cyprus, and the Himalayas and is widely cultivated in temperate areas, including the southeastern United States. All six remaining genera are represented by species native to the United States. Only two of them have no species indigenous to our area: *Larix* Miller, larch, with about ten species in northern North America and Eurasia, and *Pseudotsuga* Carr., Douglas fir, with seven or eight species in western North America and eastern Asia.

The family Pinaceae is a well-defined natural group, distinguished particularly by characters of its ovulate cones. These have well-developed scales that are distinct from the subtending bracts, two inverted ovules per scale, and a prominent terminal seed wing developing from the cone scale. It is supported as a monophyletic group by shared features unique among the gymnosperms, including the pattern of proembryogeny (Doyle, 1963; Singh), protein-type sieve-cell plastids (Behnke), and the absence of biflavonoid compounds (Geiger & Quinn).

On the basis of morphological comparisons (e.g., Eckenwalder; Hart), immunological comparisons of seed-protein extracts (Price & Lowenstein), and phloem polypeptide profiles (Alosi & Park), there is no evidence that the Pinaceae are closely related to any of the other extant families of conifers. Rather, the family has a long fossil history as a distinct lineage, probably dating to the Triassic (Miller, 1977), as is also the case for such other major extant coniferous groups as the Araucariaceae, the Podocarpaceae, and the Cupressaceae-Taxodiaceae lineage. The combination of apparently primitive characters (bisaccate pollen with two prothallial cells, chromosome number $2n = 24$, and lack of bract-scale fusion) and uniquely derived features characteristic of the Pinaceae suggests that its origin should be sought among early conifer groups preceding the extant families (see Florin, 1951). Thus a number of European workers

[3]One species, *Pinus Merkusii* Jungh & De Vries, is native from Indochina south of the Equator to Sumatra.

(e.g., Emberger; Lebreton & Sartre; Norin) have placed the Pinaceae in the unifamilial order Pinales.

The monotypic *Sciadopitys* Sieb. & Zucc., Japanese umbrella pine (Sciadopityaceae), has sometimes been associated with the Pinaceae on the basis of its unusual "double-needles." These superficially resemble longitudinally fused pairs of *Pinus* needles but in fact differ from them considerably in pattern of development (see Roth). Other morphological and cytological evidence suggests that *Sciadopitys* diverged at an early time from the cupressaceous-taxodiaceous lineage, since *Sciadopitys*—as well as the Cupressaceae *sensu lato* (including Taxodiaceae)—differs from the Pinaceae in having nonsaccate pollen without prothallial cells, substantial fusion of bract and scale in the mature ovulate cone, multiple ovules per scale, and lateral seed wings derived from the seed coat (Florin, 1951; Singh; Sporne). In its proembryogeny *Sciadopitys* appears to be more primitive than either group (Doyle & Brennan; Singh). Immunological comparisons of seed-protein extracts (Price & Lowenstein) and overall patterns of secondary-product chemistry (Hegnauer, 1962, 1986) also indicate that *Sciadopitys* is quite isolated from the Pinaceae.

The ten genera of Pinaceae are clearly delimited, but subfamilial groupings have been controversial. *Pinus,* in recognition of its unusual short-shoots (needle fascicles) and its distinctive, usually highly thickened cone scales, is often placed by itself in subfam. Pinoideae. Vierhapper and a number of later authors (e.g., Florin, 1931, 1963; Krüssmann; Pilger & Melchior) divided the remaining genera into two groups based on presence or absence of strongly condensed vegetative short-shoots that bear the majority of the foliage leaves. The genera with marked shoot dimorphism (*Cedrus, Larix, Pseudolarix*) have been placed in subfam. Laricoideae Pilger & Melchior, with the remaining genera (long-shoots only) in subfam. Abietoideae Ascherson & Graebner *emend.* Pilger & Melchior or in equivalent groups of lower rank. The relatively recently discovered genus *Cathaya,* which has less-marked shoot dimorphism (see photo in Chun & Kuang, 1958), was placed by Florin (1963) in the Abietoideae. However, other morphological characters show little concordance with shoot dimorphism, so division of the family on this basis alone is highly artificial.

Another subfamilial division, first proposed by Van Tieghem (1891), placed together those genera with resin canals in the primary root adjacent to each protoxylem pole (*Pinus, Picea, Larix, Pseudotsuga* (and *Cathaya*; see Hu & Wang), comprising the Pinées or Epixylocèles of Van Tieghem, here termed the pinoid group) and those with a single central resin canal in the primary root (*Cedrus, Tsuga, Abies, Keteleeria,* and *Pseudolarix,* comprising the Cedrées or Myélocèles of Van Tieghem, here termed the abietoid group). This classification appears to be a natural one, based on the concordance of root anatomy with other morphological features. Each of the pinoid genera regularly exhibits both vertical and horizontal resin canals in the wood and lacks resin vesicles in the seed coat, while the abietoid genera have much more localized resin canals in the wood following wounding ("traumatic resin canals," usually in the vertical system) and have resin vesicles in the seed coat (Jeffrey; Phillips; Price *et al.*). Immunological comparisons of seed-protein extracts have also yielded precisely the abietoid and pinoid groups of Van Tieghem (Prager *et al.*;

Price *et al.*). Thus recognition of two subfamilies, the Pinoideae and the Abietoideae, corresponding to the groups of Van Tieghem—or of three subfamilies, with *Pinus* placed in a monogeneric Pinoideae and the remaining pinoid genera in the Laricoideae—seems to be the most reasonable alternative.

Within the pinoid group, *Larix* and *Pseudotsuga* appear to be closely related sister-genera on the basis of their shared possession of nonsaccate pollen, a highly modified micropylar apparatus at time of pollination, fiber-sclereids in the bark, and similar, relatively asymmetric karyotypes, all of which seem to be derived characters within the family. They also group together in immunological comparisons of seed proteins (Prager *et al.*; Price *et al.*).

Chromosome counts have been obtained for all ten genera and approximately 75 percent of the species of Pinaceae (see particularly Khoshoo, 1961). The number $2n = 24$, which is apparently primitive for the conifers,[4] has been found in all but two species (*Pseudotsuga Menziesii* (Mirbel) Franco, $2n = 26$, and *Pseudolarix amabilis* (Nelson) Rehder, $2n = 44$). Counts are available for six of the remaining seven species of *Pseudotsuga*; all have $2n = 24$ (Doerksen & Ching; El-Kassaby *et al.*). Karyotypes have been obtained for all genera of the Pinaceae (see particularly Chu & Sun; Khoshoo, 1962; Kuo *et al.*; Sax & Sax; see also Saylor, 1964, 1972, 1983, cited under *Pinus*); they vary from largely symmetrical (11 of 12 chromosomes metacentric or submetacentric in *Pinus, Cathaya,* and *Cedrus*; nine of 12 metacentric in *Picea* and *Tsuga*) to extremely asymmetric in *Pseudolarix. Pseudotsuga* and *Larix* both have asymmetric karyotypes—six metacentric and six subtelocentric chromosomes, with one metacentric chromosome replaced by a subtelocentric and an additional short telocentric chromosome in *P. Menziesii. Pseudolarix amabilis* has a particularly unusual karyotype, with two metacentric and 20 shorter subtelocentric chromosomes (Sax & Sax), implying an aneuploid increase involving fission of ten of the original 12 chromosomes (Ehrendorfer; Khoshoo, 1959). Given their long fossil record, the Pinaceae have shown remarkably little change in chromosome number, a situation shared with the other conifer families except the Podocarpaceae (Ehrendorfer; Khoshoo, 1962), but one differing markedly from most angiosperm groups. Individuals or cells with polyploid chromosome numbers have occasionally been reported in the Pinaceae (Khoshoo, 1959), but polyploid plants apparently seldom survive under natural conditions.

The Pinaceae are characterized by a specialized variant of the coniferous pattern of proembryogeny (Dogra, 1980; Doyle, 1963; Singh). Two free-nuclear mitotic divisions yield four nuclei that come to lie in a more or less planar arrangement. A third mitotic division yields two tiers of four nuclei that rapidly become separated by transverse walls. The Pinaceae differ from the other conifers in that the lower of the two tiers produced by vertical division of the original upper or "open" tier does not elongate to form the suspensor. Instead, the tier of cells below this, produced by vertical division of the lowest original tier, forms the suspensor, while only the lowest of the four tiers forms the embryonal mass. In *Pseudotsuga* (at least in *P. Menziesii*) apparently only the

---

[4]This number is also found in *Taxus* (Taxaceae), *Cephalotaxus* (Cephalotaxaceae), some Podocarpaceae, and the outgroup *Ginkgo* L. (see discussions in Ehrendorfer, and Khoshoo, 1962).

lower of the original two tiers divides, yielding a three-tiered proembryo (Allen & Owens; Singh).

Although only a single embryo usually matures in each seed, polyembryony is characteristic of many conifers, including all genera of Pinaceae. Simple polyembryony, where embryos are formed in more than one archegonium per ovule, occurs relatively frequently. Cleavage polyembryony, where multiple embryos are formed by the splitting up of the products of a single zygote, is also a regular feature in *Pinus, Cathaya, Cedrus, Tsuga,* and *Keteleeria* (Doyle & Brennan; Wang & Chen). It also occurs in a limited percentage of embryos in some species of *Abies* but has not been found in *Pseudolarix, Picea, Larix,* or *Pseudotsuga.* In the last two genera, unequal growth rates often cause two of the units to overtop the others (although the four embryonal units do not separate from one another, a situation termed "incipient cleavage" by Doyle & Brennan).

The Pinaceae have the highest average number of cotyledons and the greatest range in this number of any family of seed plants (Butts & Buchholz). The highest numbers are found in *Pinus,* which has the entire range of numbers for the family (2–18, with intraspecific averages ranging from ca. 4 to 14), and in *Cedrus* (5–14, averaging ca. 9 or 10). Detailed discussions of the vascular-bundle patterns in the cotyledons and embryos are presented in Boureau (1939) and Ferré (1952).

Ovulate-cone anatomy in the Pinaceae has been studied by Aase, Miller (1976), Radais, and Van Tieghem (1869), with emphasis on distribution of the vasculature and resin canals. *Pinus* appears to be unusual in having partial fusion of the bract and scale traces at their bases. The arrangement of the resin canals associated with these traces seems to be fairly specific to each genus (Miller, 1976; Radais), with those in the cones of *Pinus* restricted to the area abaxial to the scale trace, perhaps because of the basal fusion of the traces. The axial vascular cylinder of the cone is reduced in thickness and much dissected in the genera with abscising cone scales (*Abies, Cedrus, Pseudolarix*; Miller, 1976).

Pollen grains are bisaccate in the Pinaceae, except in *Larix* and *Pseudotsuga,* where they are spheroidal and nonsaccate, and *Tsuga* sect. Tsuga, where the saccae are reduced to a subequatorial frill (G. Erdtman, 1957, 1965; Ueno). Saccate pollen is evidently the primitive state both in the Pinaceae and among the conifers generally (see Florin, 1951; Millay & Taylor), but the saccae have been lost in all other extant coniferous groups except the Podocarpaceae, where pollen may be bi-, tri-, or nonsaccate.

The Pinaceae are wind pollinated, as are the other conifers, and often release huge volumes of pollen. Specific mechanisms of pollination have been reviewed by Dogra (1964), Doyle (1945), and Singh and have recently been elegantly demonstrated through scanning electron, as well as light, microscopy for a number of western North American taxa by Owens and coworkers (Allen & Owens; Owens & Molder; and additional references cited under the individual genera). A pollination-drop mechanism has been substantiated only in *Pinus* and *Picea* and is lacking in the other genera examined to date (*Cathaya, Keteleeria,* and *Pseudolarix* are unstudied in this regard). It is found in most other

gymnosperms and is presumably the primitive state for the Pinaceae (see Doyle, 1945; Singh).

In *Pinus* and *Picea,* pollen is caught on a sticky film on the inner surfaces of the two integumentary arms and, when contacted by the pollination drop, is then drawn into the micropylar canal, after which it floats or is pulled up to the nucellus (Owens *et al.,* 1981, 1987, cited under *Pinus* and *Picea,* respectively). *Pseudotsuga* and *Larix* have a highly specialized mechanism in which the unwinged pollen is caught between hairs on the highly expanded outer-integument lip and then drawn into the micropylar canal by collapse of the surface of the lip (Allen & Owens; Owens & Molder). In *Cedrus* and *Abies,* pollen is caught on the inner surface of the funnel-shaped integumentary area around the micropyle, and the nucellus grows out to the pollen (Doyle, 1945; Owens & Molder, 1977, cited under *Abies*). In *Tsuga Mertensiana* (Bong.) Carr., of sect. HESPEROPEUCE, the situation is similar, but the integument tip is very asymmetric; in sect. TSUGA the pollen lands primarily on the bract surfaces rather than the ovule tip, and then the pollen tubes grow over to the nucellus (Doyle & O'Leary). This unusual situation is otherwise seen only in the Araucariaceae and in *Saxegothaea* Lindley (Podocarpaceae), which also have unwinged pollen (Doyle, 1945). Doyle (1945) related the pollination mechanisms of Pinaceae to the groupings of Van Tieghem (1891) in an evolutionary diagram, showing series leading from *Pinus* and *Picea* to *Larix* and *Pseudotsuga* on the one hand, and *Cedrus, Abies,* and *Tsuga* on the other. *Cathaya* might be expected to have a mechanism similar to that of *Pinus* and *Picea,* and *Keteleeria* and *Pseudolarix* to have ones similar to those of the other abietoid genera.

A characteristic feature of the Pinaceae is the formation of ectomycorrhizal associations with a variety of fungi, including a number of basidiomycetes, such as *Armillaria matsutake* and *Boletus edulis,* that are highly sought for their edible mushrooms. The presence of mycorrhizae appears to help buffer the plants against various types of environmental stress, and thus mycorrhizal associations have been much investigated in regard to commercial tree production.

Because of the economic importance of the Pinaceae, numerous studies of the chemical composition of the leaves, wood, and bark have been made on many species (see reviews by Hegnauer, 1962, 1986; Norin; Squillace; Von Rudloff), with particular emphasis on *Pinus, Picea, Abies,* and *Pseudotsuga.* The chemistry of *Cedrus* has recently been reviewed by Agrawal & Rastogi. Significant gaps remain in our knowledge of the chemosystematics of even the best-known genera, however.

The Pinaceae contain a diversity of terpenoid compounds in the bark, wood, leaves, and cones, particularly in the characteristic oleoresins of the resin canals or vesicles. The bulk of the volatile portion of the stem and leaf oleoresins is usually a complex mixture of monoterpenes. These impart much of the characteristic fragrance associated with Pinaceae. Terpenoid and hydrocarbon profiles of the oleoresins or turpentines (the steam-distillable portion thereof) often show significant differences among species and have been widely used in chemosystematics of the Pinaceae (see particularly the reviews by Squillace and

Von Rudloff and the papers by Mirov, Von Rudloff, Zavarin, and their co-workers cited under the individual genera).

Sesquiterpenoid compounds have received much less attention than mono-terpenoids, although the former may also be of considerable chemosystematic utility. *Cedrus* is particularly notable for its array of unusual structural types including the atlantones, himachalenes, and allohimachalenes (Agrawal & Rastogi; Norin).

Diterpene resin acids are major constituents of the "rosin" remaining after removal of the volatile components of pinaceous oleoresin by steam distillation (Hegnauer, 1962, 1986; Norin). Resin acids of the abietane and pimarane types have been reported from woods of *Pinus, Picea, Larix, Pseudotsuga,* and *Abies* (H. Erdtman, 1963; Norin) and from the cone oleoresins of *Cedrus* (Norin). These compounds are to be expected in the other genera if appropriate oleo-resins are examined. Both pimarane and abietane terpenoids occur widely in the conifers (Hegnauer, 1986), although the abietane type was once thought to be specific to the Pinaceae (H. Erdtman, 1963). Several other types of diter-penoids have also been found in the Pinaceae, including labdane terpenoids in various species of *Pinus, Picea, Larix,* and *Abies,* and macrocyclic compounds of the thunbergene type in *Pinus, Picea, Larix,* and *Pseudotsuga* (Norin). Pseu-dolaric acids, a very unusual structural class of diterpenes, have been isolated from the roots of *Pseudolarix amabilis*; these constitute the active components of antifungal medicines in traditional use in China (Zhou *et al.*).

Serratene triterpenoids are characteristic bark components of *Pinus* and *Picea* (Hegnauer, 1962, 1986; Norin) and the morphologically similar *Cathaya* (He *et al.*) but have not been found in the other genera. Unusual lanostane triter-penoids have been isolated from the bark or needles of a few species of *Abies* (Hegnauer, 1962, 1986; Norin), while other tetracyclic triterpenes have been found in *Larix, Pseudotsuga, Pinus,* and *Picea.*

Alkaloids do not occur frequently in the Pinaceae but have been detected in some species of *Pinus, Picea,* and *Keteleeria* (Hegnauer, 1962; Willaman & Schubert). The pyridine alkaloids pinidine and α-pipecoline have been isolated from needles of several species of *Pinus* but are apparently absent in many others.

The Pinaceae are unusual in their almost total lack of biflavonoid com-pounds, otherwise ubiquitous among the conifers and *Ginkgo* (Geiger & Quinn). A single biflavonoid compound, abiesin, has recently been reported to occur in low concentration in the needles of *Abies spectabilis* (D. Don) Spach (Heg-nauer, 1986).

Anthocyanins (3-glucosides of cyanidin (red) and delphinidin (blue), either singly or in combination) are important in the coloration of the young pollen and seed cones of the Pinaceae (Santamour, 1966). They are also involved in the transient spring coloration of *Picea* needles (Santamour, 1967).

Cyclitols (sugar 5-methyl ethers) such as sequoyitol and pinitol occur widely among the conifers, including the Pinaceae, and are of interest in that pinitol is the sugary substance exuded from the trunk of sugar pine (*P. Lambertiana* Douglas) and the related *P. Ayacahuite* Ehrenberg (Hegnauer, 1962). The re-lated compound D-1-O-methylmucoinositol occurs widely in the leaves of the

other families of conifers but is apparently absent in those of the Pinaceae (Dittrich *et al.*).

Jamieson & Reid surveyed the fatty acids of conifer leaves, including representatives of seven genera of the Pinaceae. These uniformly exhibited a series of 18-carbon polyunsaturated acids that were absent in the other conifers examined.

Many species of Pinaceae are of great economic importance, with the family supplying over half of the world's timber (Sporne). *Pinus, Pseudotsuga, Picea, Larix, Abies, Tsuga,* and *Cedrus* are all of major significance in this regard. These genera are important sources of ornamental trees, and numerous horticultural varieties have been developed (L. H. Bailey; Dallimore & Jackson; Den Ouden & Boom; Krüssmann). The attractive golden larch (*Pseudolarix amabilis*), grown as an ornamental in China, is suitable to much of our region. Species of *Abies* (e.g., *A. balsamea* and *A. Fraseri*), *Picea,* and *Pinus* are frequently used as Christmas trees. The Pinaceae, particularly *Pinus,* are also economically important as the source of turpentine, pitch, and rosin used in shipbuilding (often termed "naval stores"), as well as in other industries. In addition, the leaf and stem resins of several genera have been used by native peoples of the United States and Canada in treating respiratory ailments and aiding wound healing, as well as for other medicinal purposes (Arnason *et al.*; Krochmal & Krochmal).

REFERENCES:

AASE, H. C. Vascular anatomy of the megasporophylls of conifers. Bot. Gaz. **60:** 277–313. 1915.

AGRAWAL, P. K., & R. P. RASTOGI. Chemistry of true cedars. Biochem. Syst. Ecol. **12:** 133–144. 1984. [*Cedrus.*]

ALLEN, G. S., & J. N. OWENS. The life history of Douglas fir. x + 139 pp. Ottawa, Canada. 1972. [*Pseudotsuga Menziesii*; numerous illustrations, including seven color plates.]

ALOSI, M. C., & R. B. PARK. A survey of phloem polypeptides in conifers. Curr. Topics Pl. Biochem. Physiol. **2:** 250. 1983.

ARNASON, T., R. J. HEBDA, & T. JOHNS. Use of plants for food and medicine by native peoples of eastern Canada. Canad. Jour. Bot. **59:** 2189–2325. 1981. [Pinaceae, 2202, 2216, 2315–2317.]

BAILEY, I. W. The structure of wood in the Pineae. Bot. Gaz. **48:** 47–55. *pl. 5.* 1909.

BAILEY, L. H. The cultivated conifers in North America. ix + 404 pp. *158 pls.* New York. 1933.

BAILLON, H. Conifères. Hist. Pl. **12:** 1–45. 1894. [Pinaceae, 16–22, 27–29, 44.]

BANNAN, M. W. Vertical resin ducts in the secondary wood of the Abietineae. New Phytol. **35:** 11–46. *pl. 1.* 1936. [Results of experimental wounding on resin-canal distribution in Pinaceae; response is greater in pinoid than in abietoid genera.]

BARNER, H., & H. CHRISTIANSEN. The formation of pollen, the pollination mechanism, and the determination of the most favorable time for controlled pollinations in *Larix.* Silvae Genet. **9:** 1–11. 1960.

BEAN, W. J. Trees and shrubs hardy in the British Isles. ed. 8. 4 vols. London. 1970–1980. [*Abies,* 1: 143–169; *Picea,* 3: 176–199; *Pinus,* 3: 209–248; *Tsuga,* 4: 622–630.]

BEHNKE, H.-D. Sieve element plastids of Gymnospermae: their ultrastructure in relation to systematics. Pl. Syst. Evol. **123:** 1–12. 1974. [Protein-type plastids seen only in Pinaceae.]

BENTHAM, G., & J. D. HOOKER. Abietineae. Gen. Pl. 3(1): 438–442. 1880. [Pinaceae.]

Bobrov, E. G. On intergeneric hybridization in the family Pinaceae. (In Russian; English summary.) Bot. Zhur. **68:** 857–865. 1983. [Forestry Abstr. **48:** 564. 1987; suggests origins of pinaceous taxa—e.g., portions of *Larix, Picea,* and *Tsuga*—by this mechanism; needs independent experimental verification.]

Boureau, E. Recherches anatomiques et expérimentales sur l'ontogénie des plantules des Pinacées et ses rapports avec la phylogénie. Ann. Sci. Nat. Bot. XI. **1:** 1–219. 1939.

Buchholz, J. T. Polyembryony among Abietineae. Bot. Gaz. **69:** 153–167. 1920. [See also Am. Jour. Bot. **7:** 125–145. 1920.]

————. The pine embryo and the embryos of related genera. Trans. Illinois Acad. Sci. **23:** 117–125. 1931.

————. A comparison of the embryogeny of *Picea* and *Abies*. Madroño **6:** 156–167. 1942.

————. Generic and subgeneric distribution of the Coniferales. Bot. Gaz. **110:** 80–91. 1948.

Butts, D., & J. T. Buchholz. Cotyledon number in conifers. Trans. Illinois Acad. Sci. **33:** 58–62. 1940. [Data from population samples; literature review.]

Campo, M. van, & J. Sivak. Structure alvéolaire des pollens à ballonets des Abiétacées. Pollen Spores **14:** 115–141. 1972. [Alveolar structure of pollen saccae in the Pinaceae.]

Campo-Duplan, M. van. Recherches sur la phylogénie des Abiétinées d'après leurs grains de pollen. Trav. Lab. Forest. Toulouse, Tome II, Sect. I, Vol. IV, Art. I: 1–186. 1950.

Carrière, E. A. Traité général des conifères. ed. 2. xii + 910 pp. Paris. 1867. [Pinaceae, 239–589; first treatment to use the nine known genera with their modern circumscriptions; *Tsuga* raised to rank of genus in ed. 1 (1855).]

Chamberlain, C. J. Gymnosperms: structure and evolution. xi + 484 pp. Chicago. 1935.

Chang, Y.-P. Bark structure of North American conifers. U. S. Dep. Agr. Tech. Bull. **1095.** ii + 86 pp. 1954. [Pinaceae, 12–48, *figs. 3–28*; detailed anatomical comparisons for six genera; numerous photomicrographs; keys to genera.]

Cheng, W.-C., & L.-K. Fu, eds. Gymnospermae. (In Chinese; nomenclatural portions primarily in English and Latin.) Fl. Reipubl. Pop. Sinicae 7. xiv + 544 pp. 1978. [Pinaceae, 32–281; significant new treatments of the Chinese species, including *Keteleeria* (9 species) and *Tsuga* (5 species); many useful illustrations of little-known taxa.]

Chowdhury, C. R. The morphology and embryology of *Cedrus Deodara* (Roxb.) Loud. Phytomorphology **11:** 283–304. 1961.

————. The embryogeny of conifers: a review. *Ibid.* **12:** 313–338. 1962.

Chowdhury, K. A. *Abies* and *Picea*: morphological studies. Council of Sci. and Industr. Res., Bot. Monogr. 9. viii + 46 pp. New Delhi. 1974. [Critical review, Phytomorphology **25:** 124. 1974.]

Christiansen, H. The formation of pollen, the pollination mechanism, and the determination of the most favorable time for controlled pollination in *Pseudotsuga Menziesii*. Silvae Genet. **11:** 89–124. 1962. [See also *Ibid.* **18:** 97–104. 1969, which contains the unusual claim that the male gametes are unique among conifers in being ciliated and rapidly motile; needs verification.]

Chu, C. A brief introduction to the Chinese species of the genus *Pseudotsuga*. Davidsonia **12:** 15–17. 1981. [Key, map, and distributional information; five species recognized for China and eight worldwide.]

Chu, C.-C., & C.-S. Sun. Chromosome numbers and morphology in *Cathaya*. (In Chinese; English summary.) Acta Phytotax. Sinica **19:** 444–446. 1981. [$2n = 24$.]

Chun, W.-Y., & K.-Z. Kuang. A new genus of Pinaceae—*Cathaya* Chun et Kuang, *gen. nov.*, from southern and western China. (In Russian and Latin; English summary.) Bot. Zhur. **43:** 461–476. 1958. [Extensive illustrations; see also the later

treatment in Acta Bot. Sinica **10**: 245, 246. *pls. 1–3.* 1962, in which one of the two original species is placed in synonymy.]

COKER, W. C., & H. R. TOTTEN. Trees of the southeastern states. ed. 3. viii + 419 pp. Chapel Hill, North Carolina. 1945. [Pinaceae, 15–42.]

COULTER, J. M., & C. J. CHAMBERLAIN. Morphology of gymnosperms. ed. 2. xi + 466 pp. Chicago. 1917.

CRITCHFIELD, W. B. Impact of the Pleistocene on the genetic structure of North American conifers. Pp. 70–118 *in* R. M. LANNER, ed., Proceedings of the Eighth North American Forest Biology Workshop. Logan, Utah. 1984. [Reviews variation in electrophoretic alleles, terpenoids, and morphology for selected species of *Picea, Abies, Pinus,* and *Pseudotsuga.*]

DALLIMORE, W., & A. B. JACKSON. A handbook of Coniferae and Ginkgoaceae. ed. 4 (revised by S. G. HARRISON). xix + 729 pp. *46 pls.* London. 1966.

DEN OUDEN, P., & B. K. BOOM. Manual of cultivated conifers. x + 2 unnumbered + 526 pp. The Hague. 1965.

DICKINSON, T., P. KNOWLES, & W. H. PARKER. Data set congruence in northern Ontario tamarack (*Larix laricina,* Pinaceae). Syst. Bot. **13**: 442–455. 1988. [Compares morphometric and isozyme data.]

DITTRICH, P., M. GIETL, & O. KANDLER. D-1-O-methyl-mucoinositol in higher plants. Phytochemistry **11**: 245–250. 1971. [Absent from the leaves of Pinaceae.]

DOERKSEN, A. H., & K. K. CHING. Karyotypes in the genus *Pseudotsuga.* Forest Sci. **18**: 66–69. [2*n* = 24 in five Asian species.]

DOGRA, P. D. Pollination mechanisms in gymnosperms. Pp. 142–175 *in* P. K. K. NAIR, ed., Advances in palynology. Lucknow. 1964. [General review relying heavily on work of DOYLE.]

————. Embryogeny of gymnosperms and taxonomy—an assessment. Glimpses in Plant Research **5**: 114–128. 1980.

DOYLE, J. Developmental lines in pollination mechanisms in the Coniferales. Sci. Proc. Roy. Dublin Soc. **24**: 43–62. 1945. [Evolutionary interpretation of pollination mechanisms in Pinaceae.]

————. Proembryogeny in *Pinus* in relation to that in other conifers—a survey. Proc. Irish Acad. B. **62**: 181–216. 1963.

———— & M. BRENNAN. Cleavage polyembryony in conifers and taxads—a survey II. Cupressaceae, Pinaceae and conclusions. Sci. Proc. Roy. Dublin Soc. A. **4**: 137–158. 1972.

———— & A. KANE. Pollination in *Tsuga Pattoniana* and in species of *Abies* and *Picea.* Sci. Proc. Roy. Dublin Soc. II. **23**: 57–70. *pls. 2, 3.* 1943. [*T. Pattoniana* = *T. Mertensiana* (Bong.) Carr.]

———— & M. O'LEARY. Pollination in *Tsuga, Cedrus, Pseudotsuga* and *Larix.* Sci. Proc. Roy. Dublin Soc. II. **21**: 191–204. *pls. 4, 5.* 1935.

ECKENWALDER, J. E. Re-evaluation of Cupressaceae and Taxodiaceae: a proposed merger. Madroño **23**: 237–256. 1976. [Comparisons among the families of conifers.]

EHRENDORFER, F. Evolutionary significance of chromosomal differentiation patterns in gymnosperms and primitive angiosperms. Pp. 220–240 *in* C. B. BECK, ed., Origin and early evolution of angiosperms. New York. 1976.

EICHLER, A. W. Coniferae. *In:* A. ENGLER & K. PRANTL, Nat. Pflanzenfam. II. **1**: 28–116. 1889. [With contributions by ENGLER and PRANTL.]

EL-KASSABY, Y. A., A. M. COLANGELLI, & O. SZIKLAI. A numerical analysis of karyotypes in the genus *Pseudotsuga.* Canad. Jour. Bot. **61**: 536–544. 1983. [Compares karyotypes of all species except *P. brevifolia* Cheng & Fu.]

———— & E. E. WHITE. Isozymes and forest trees: an annotated bibliography. Canad. Forest Serv. Pacific Forest Res. Ctr. Info. Rep. **BC-X-267.** 1985.*

EMBERGER, L. Gymnospermes. Traité de botanique systématique **2**(1): 383–459. 1960. [Pinaceae placed in a monofamilial Pinales.]

ERDTMAN, G. Pollen and spore morphology/plant taxonomy. Vol. 2. Gymnospermae,

Pteridophyta and Bryophyta (illustrations). *Frontisp.* + iv + 151 pp. *5 pls.* Stockholm. 1957. [Pinaceae, 6, 7, 10, 11, 13, 27, 28, 32–36, 39, 40, 43, 44.] Vol. 3. Gymnospermae, Bryophyta (text). 191 pp. *24 pls.* Stockholm. 1965. [Pinaceae, 11, 13, 14, 22–25, 45–48, 54–60, 69–71, 78–80; *pls. 1, 8–19, 21.*]

ERDTMAN, H. Conifer chemistry and taxonomy of conifers. Pp. 1–27 *in* K. KRATZL & G. BILLEK, eds., Proceedings of the Fourth International Congress of Biochemistry, Vienna, 1958. Vol. 2. New York. 1959. [Pinaceae, 2–12.]

————. Some aspects of chemotaxonomy. Pp. 88–125 *in* T. SWAIN, ed., Chemical plant taxonomy. London. 1963. [See particularly pp. 106–112.]

FERRÉ, Y. DE. Les formes de jeunesse des Abiétacées. Trav. Lab. Forest. Toulouse, Tome II, Sect. I, Vol. III, Art. I: 1–284. 1952. [Morphology of cotyledons and primary and secondary leaves compared.]

———— & H. GAUSSEN. Le rameau phylétique: *Pinus, Pseudolarix, Keteleeria.* Bull. Soc. Hist. Nat. Toulouse **80:** 108–118. 1945. [Reprinted as Trav. Lab. Forest. Toulouse, Tome I, Vol. IV, Art. VIII: 1–11. 1945.]

FITSCHEN, J. Handbuch der Nadelholzkunde. xv + 765 pp. Berlin. 1930. [Revised 3rd ed. of BEISSNER's Handbuch der Nadelholzkunde.]

FLORIN, R. Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. Sv. Vet.-akad. Handl. III. **10:** 1–588. *pls. 1–58.* 1931. [Classic treatment of vegetative anatomy of the conifers; Pinaceae, 93–111, 306–347, *pls. 34–39*; generic relationships and classification of the Pinaceae, 476–483.]

————. Evolution in cordaites and conifers. Acta Horti Berg. **15:** 285–388. 1951. [Classic study of the evolution of the coniferous ovulate cone; see also Biol. Rev. **19:** 367–389. 1954.]

————. The systematics of the gymnosperms. Pp. 323–403 *in* E. L. KESSEL, ed., A century of progress in the natural sciences, 1853–1953. San Francisco. 1955. [Historical review, mostly of morphology.]

————. The distribution of conifer and taxad genera in time and space. Acta Horti Berg. **20**(4): 121–312. 1963.

FLOUS, F. Classification et évolution d'une groupe d'Abiétinées. Trav. Lab. Forest. Toulouse, Tome I, Vol. II, Art. XVII: 1–286. 1936. [Classification, with useful historical discussion; putative evolutionary relationships in the Pinaceae; see also *Ibid.,* Tome I, Vol. III, Art. I: 1–16. 1938.]

FOWELLS, H. A., compiler & reviser. Silvics of forest trees of the United States. U. S. Dep. Agr. Agr. Handb. **271.** vi + 762 pp. 1965. [Maps by E. L. LITTLE, JR.]

GAUSSEN, H. Abiétacées. *In:* Les gymnospermes: actuelles et fossiles. Trav. Lab. Forest. Toulouse, Tome II, Sect. I, Vol. I, Chap. XI: 1–716. 1960–1967. [*Pinus* (fasc. VI), 1–272. 1960; *Pinus* (suite), *Cedrus, Abies* (fasc. VII), 273–480. 1964; *Pseudolarix, Keteleeria, Larix, Pseudotsuga, Pityites, Picea, Cathaya, Tsuga* (fasc. VIII), 481–672. 1966; Additions et corrections (fasc. IX), 673–716. 1967; Bibliographie, Tome II, Vol. I, Partie III: 1–180. 1979 (bibliography for the entire work).]

GEIGER, H., & C. QUINN. Biflavonoids. Pp. 692–742 *in* J. B. HARBORNE, T. J. MABRY, & H. MABRY, eds., The flavonoids, pt. 2. London. 1975. [Pinaceae unique among conifers in lacking biflavonoids.]

GIANNASI, D. E., & D. J. CRAWFORD. Biochemical systematics II. A reprise. Evol. Biol. **26:** 25–248. 1986. [Terpenoids in Pinaceae, pp. 66–71.]

GREGUSS, P. Identification of living gymnosperms on the basis of xylotomy. 263 pp. *350 pls., 8 tables.* Budapest. 1955. [Pinaceae, 183–249, *pls. 196–345.*]

————. Xylotomy of the living conifers. 172 + 329 pp. Budapest. 1972. [Pinaceae, 109–159, *pls. 10, 115–165, figs. 95–145*; an extension of GREGUSS, 1955.]

HAMRICK, J. L., J. B. MITTON, & Y. B. LINHART. Levels of genetic variation in trees: influence of life history characters. Pp. 35–41 *in* M. T. CONKLE, tech. coord., Proceedings of the Symposium on Isozymes of North American Forest Trees and Forest Insects. U. S. Dep. Agr. Gen. Tech. Rep. **PSW-48.** 1981. [Compares isozyme variability in *Abies, Picea, Pinus,* and *Pseudotsuga.*]

HARDIN, J. W. Studies of the southeastern United States flora. II. The gymnosperms. Jour. Elisha Mitchell Sci. Soc. **87**: 43–50. 1971. [Keys; valuable commentary on Pinaceae.]

HART, J. A. A cladistic analysis of conifers: preliminary results. Jour. Arnold Arb. **68**: 269–307. 1987. [Both intergeneric and interfamilial cladograms; character states tabulated for all genera of Pinaceae.]

HE, G.-F., Z.-W. MA, W.-F. YIN, & M.-L. CHENG. On serratene components in relation to the systematic position of *Cathaya* (Pinaceae). Acta Phytotax. Sinica **19**: 440–443. 1981. [Found in bark of *Cathaya, Pinus,* and *Picea.*]

HEGNAUER, R. Chemotaxonomie der Pflanzen. Band 1. Thallophyten, Bryophyten, Pteridophyten und Gymnospermen. 517 pp. Basel and Stuttgart. 1962. [Pinaceae, 373–410, 480, 481.] Band 7. Nachträge zu Band 1 und Band 2. xii + 804 pp. 1986. [Pinaceae, 504–523, 801; extensive literature review.]

HICKEL, R. Graines et plantules des conifères. Bull. Soc. Dendrol. France **19**: 13–115; **20**: 134–204. 1911. [Pinaceae, 52–115 (seeds), 163–204 (seedlings).]

HILL, T. G., & E. DE FRAINE. On the seedling structure of gymnosperms. II. Ann. Bot. **23**: 189–227. *pl. XV.* 1909.

HO, R.-H., & O. SZIKLAI. On the pollen morphology of *Picea* and *Tsuga* species. Grana Palynol. **12**: 31–40. 1972. [Emphasizes morphology of *T. Mertensiana* in comparison to that of other taxa.]

HU, Y. S., & F. H. WANG. Anatomical studies of *Cathaya* (Pinaceae). Am. Jour. Bot. **71**: 727–735. 1984. [Thorough treatment of vegetative features and comparison with other genera.]

——— & B. J. YAO. Transfusion tissue of gymnosperm leaves. Bot. Jour. Linn. Soc. **83**: 263–272. 1981.

HUNTLEY, B., & H. J. B. BIRKS. An atlas of past and present pollen maps for Europe: 0–13000 years ago. xiv + 667 pp. Cambridge, England. 1983. [*Abies,* 22, 73–89; *Larix,* 35, 253–263; *Picea,* 39, 285–305; *Pinus,* 41, 42, 306–336.]

JAMIESON, G. R., & E. H. REID. The leaf lipids of some conifer species. Phytochemistry **11**: 269–275. 1972. [Includes seven genera of Pinaceae.]

JEFFREY, E. C. The comparative anatomy and phylogeny of the Coniferales. Part 2. The Abietineae. Mem. Boston Soc. Nat. Hist. **6**: 1–37. 1905. [Wood anatomy of Pinaceae supports the groupings of VAN TIEGHEM; groups treated as tribes Abieteae and Pineae.]

KHOSHOO, T. N. Polyploidy in gymnosperms. Evolution **13**: 24–39. 1959. [A very rare intraspecific phenomenon in Pinaceae.]

———. Chromosome numbers in gymnosperms. Silvae Genet. **10**: 1–9. 1961. [Comprehensive summary of the literature.]

———. Cytogenetical evolution in the gymnosperms—karyotype. Pp. 119–135 *in* P. MAHESHWARI, B. M. JOHRI, & I. K. VASIL, eds., Proceedings of the Summer School of Botany, Darjeeling. New Delhi. 1962.

KONAR, R. N., & R. NAGMANI. Female gametophyte and embryogeny in *Picea Smithiana* and *Abies Pindrow* (Pinaceae). Bot. Jahrb. **101**: 267–297. 1980.

——— & Y. P. OBEROI. Recent work on reproductive structures of living conifers and taxads—a review. Bot. Rev. **35**: 89–116. 1969. [Pinaceae, 90–95.]

KROCHMAL, A., & C. KROCHMAL. A field guide to medicinal plants. vii + 274 pp. New York. 1984.

KRÜSSMANN, G. Handbuch der Nadelgehölze. ed. 2 (revised by H.-D. WARDA). 6 unnumbered + 396 pp. *160 pls.* Berlin and Hamburg. 1983. [Also published in English as Manual of cultivated conifers (M. E. EPP, translator). 361 pp. *160 pls.* Portland, Oregon. 1985.]

KUO, S. R., T. T. WANG, & T. C. HUANG. Karyotype analysis of some Formosan gymnosperms. Taiwania **17**: 66–80. 1972. [Includes *Keteleeria, Tsuga, Pseudotsuga, Picea,* and *Pinus.*]

LEBRETON, P., & J. SARTRE. Les pinales, considerées d'un point de vue chimiotaxinomique. Canad. Jour. Forest Res. **13**: 145–154. 1983. [Flavonoids in representatives of nine genera of Pinaceae.]

LI, H. L. Present distribution and habitats of the conifers and taxads. Evolution **7**: 245–261. 1953.

LITTLE, E. L., JR. Atlas of United States trees. Vol. 1. Conifers and important hardwoods. U. S. Dep. Agr. Forest Serv. Misc. Publ. **1146**. v + 9 pp. *2 base maps, 200 species maps, 9 overlay maps.* 1971. [Detailed range maps for all American species of Pinaceae.]

———. Checklist of United States trees (native and naturalized). U. S. Dep. Agr. Forest Serv. Agr. Handb. **531**. iv + 375 pp. 1979.

———. The Audubon Society field guide to North American trees. Eastern region. 714 pp. New York. 1980.

LOTOVA, L. I. On the correlation of the anatomical features of the wood and phloem in the Pinaceae. (In Russian.) Vestn. Moskov. Univ. Biol. 6. **1**: 41–51. 1975.

MAHESHWARI, P., & H. SINGH. The female gametophyte of gymnosperms. Biol. Rev. **42**: 88–130. 1967.

MEHRA, P. N., & T. N. KHOSHOO. Cytology of conifers. I. Jour. Genet. **54**: 165–180. *pl. 5.* 1956. [Chromosome counts and karyotypes in *Pinus, Cedrus, Picea,* and *Abies*; all *n* = 12.]

MERGEN, F. Microsporogenesis and macrosporogenesis in *Pseudolarix amabilis.* Silvae Genet. **25**: 183–188. 1976.

MILLAY, M. A., & T. N. TAYLOR. Evolutionary trends in fossil gymnosperm pollen. Rev. Palaeobot. Palynol. **21**: 65–91. 1976.

MILLER, C. N., JR. Early evolution in the Pinaceae. Rev. Palaeobot. Palynol. **21**: 101–117. 1976. [Compares ovulate-cone anatomy of extant and fossil genera.]

———. Mesozoic conifers. Bot. Rev. **43**: 217–280. 1977.

———. Current status of Paleozoic and Mesozoic conifers. Rev. Palaeobot. Palynol. **37**: 99–114. 1982. [Preliminary phylogenetic comparisons of fossil and extant genera based on ovulate-cone characters alone.]

———. *Pityostrobus pubescens,* a new species of pinaceous cones from the Late Cretaceous of New Jersey. Am. Jour. Bot. **72**: 520–529. 1985. [Includes anatomical comparisons of the extant genera of Pinaceae.]

MIRANDA, V., & M. CHAPEKHAR. SEM study of the inner periclinal surface of leaf cuticles in the family Pinaceae. Bot. Jour. Linn. Soc. **81**: 61–78. 1980.

NIEMANN, G. J., & H. H. VAN GENDEREN. Chemical relationships between Pinaceae. Biochem. Syst. Ecol. **8**: 237–240. 1980. [Compares flavonoid "fingerprints" of species in nine genera.]

NORIN, T. Some aspects of the chemistry of the order Pinales. Phytochemistry **11**: 1231–1242. 1972. [Valuable review emphasizing wood-extractive chemistry of the Pinaceae.]

OWENS, J. N., & M. MOLDER. Sexual reproduction of *Larix occidentalis.* Canad. Jour. Bot. **57**: 2673–2690. 1979.

——— & S. SIMPSON. Pollen from conifers native to British Columbia. Canad. Jour. Forest Res. **16**: 955–967. 1986. [SEM and LM photographs and descriptions; includes *Abies, Tsuga, Pseudotsuga, Larix, Picea,* and *Pinus.*]

PANT, D. D., & N. BASU. A comparative study of the leaves of *Cathaya argyrophylla* Chun & Kuang and three species of *Keteleeria* Carrière. Bot. Jour. Linn. Soc. **75**: 271–282. 1977.

PARLATORE, P. Coniferae. DC. Prodr. **16**(2): 361–521. 1868. [Pinaceae, 364, 365, 377–431.]

PHILLIPS, E. W. J. Identification of softwoods by their microscopic structure. Dep. Sci. Industr. Res. London Forest Prod. Res. Bull. **22**. iii + 56 pp. *3 pls.* 1948. [Excellent comparative treatment of wood anatomy for all genera except *Cathaya*; a similar account in Jour. Linn. Soc. Bot. **52**: 259–320. 1941.]

PILGER, R. Pinaceae. *In:* A. ENGLER, Nat. Pflanzenfam. ed. 2. **13:** 271–342. 1926. [Definitive separation of Pinaceae from Taxodiaceae and Cupressaceae; introduction of the modern system of families.]

────── & H. MELCHIOR. Gymnospermae. *In:* H. MELCHIOR, Engler's Syllabus Pflanzenfam. ed. 12. **1:** 312–344. 1954. [Pinaceae, 329–332, *figs. 132, 133.*]

PRAGER, E. M., D. P. FOWLER, & A. C. WILSON. Rates of evolution in conifers (Pinaceae). Evolution **30:** 637–649. 1976. [Immunological comparison and electrophoretic characterization of seed proteins.]

PRICE, R. A., & J. M. LOWENSTEIN. An immunological comparison of the Sciadopityaceae, Taxodiaceae, and Cupressaceae. Syst. Bot. (in press). [Seed-protein extracts compared by radioimmunoassay; *Sciadopitys* relatively isolated and not close to Pinaceae.]

──────, J. OLSEN-STOJKOVICH, & J. M. LOWENSTEIN. Relationships among the genera of Pinaceae: an immunological comparison. Syst. Bot. **12:** 91–97. 1987. [Immunological comparison of seed proteins supports the classification of VAN TIEGHEM (1891).]

RADAIS, M. L. Anatomie comparée du fruit des conifères. Ann. Sci. Nat. Bot. VII. **19:** 165–368. *pls. 1–15.* 1894. [Emphasizes vascular anatomy of the ovulate cone.]

RADFORD, A. E., H. E. AHLES, & C. R. BELL. Manual of the vascular flora of the Carolinas. lxi + 1183 pp. Chapel Hill, North Carolina. 1968. [Pinaceae, 34–40; dot maps, illustrations.]

REHDER, A. Manual of cultivated trees and shrubs hardy in North America, exclusive of the subtropical and warmer temperate regions. ed. 2. xxx + 996 pp. New York. 1940. [Pinaceae, 8–47.]

──────. Bibliography of cultivated trees and shrubs hardy in the cooler temperate regions of the Northern Hemisphere. xl + 825 pp. Jamaica Plain, Massachusetts. 1949. [Detailed nomenclatural treatment; Pinaceae, 6–41.]

ROTH, I. Histogenese und morphologische Deutung der Doppelnadeln von *Sciadopitys.* Flora **152:** 1–23. 1962. ["Double-needles" of *Sciadopitys* are not comparable to a fused pair of needles.]

SANTAMOUR, F. S., JR. New chromosome counts in *Pinus* and *Picea.* Silvae Genet. **9:** 87, 88. 1960. [*Picea* (15 species) and *Pinus* (12 species), all *n* = 12.]

──────. Anthocyanins of conelets in the Pinaceae. Forest Sci. **12:** 429–431. 1966.

──────. Anthocyanins in spruce foliage. Bull. Morris Arb. **18:** 41, 42. 1967.

SARGENT, C. S. Silva of North America. Vol. 11. *Pinus.* vii + 163 pp. *pls. 538–592.* Boston and New York. 1897 [1898]. Vol. 12. Abietineae after *Pinus.* vii + 144 pp. *pls. 593–620.* Boston and New York. 1898 [1899]. [Excellent illustrations of *Abies, Picea, Pinus, Tsuga, Pseudotsuga,* and *Larix*; much useful information about utilization of the genera.]

SAX, K., & H. J. SAX. Chromosome number and morphology in the conifers. Jour. Arnold Arb. **14:** 356–374. *pl. 75.* 1933. [Chromosome numbers and karyotypes for most genera of Pinaceae.]

SCHOPF, J. M. The embryology of *Larix.* Illinois Biol. Monogr. **19**(4): 1–97. 1943.

SEITZ, F. W. Chromosomenzahlenverhältnisse bei Holzpflanzen. Silvae Genet. **1:** 22–32. 1951. [Review of chromosome counts, mainly from the literature; includes a few otherwise-unpublished counts by the author for *Abies* and *Picea* (all *n* = 12).]

SIMAK, M. Karyotype analysis of *Larix Griffithiana* Carr. Hereditas **56:** 137–141. 1966. [See also Stud. Forest. Suecica **17:** 1–15. 1964.]

SINGH, H. Embryology of gymnosperms. Band 10, Teil 2 *in* K. LINSBAUER, Handbuch der Pflanzenanatomie. ed. 2. xii + 302 pp. Berlin. 1978. [Male and female gametophytes; pollination mechanisms; embryogeny; extensive bibliography.]

SIVAK, J. Les caractères de diagnose des graines de pollen à ballonets. Pollen Spores **17:** 349–421. 1975. [Extensive scanning electron microscopic comparisons of pinaceous pollen.]

SMALL, J. K. Manual of the southeastern flora. xxii + 1554 pp. New York. 1933. [Pinaceae, 3–8.]

SNAJBERK, K., & E. ZAVARIN. Mono- and sesqui-terpenoid differentiation of *Pseudotsuga* of the United States and Canada. Biochem. Syst. Ecol. **4**: 159–163. 1976. [Cortical oleoresin composition of *P. macrocarpa* and *P. Menziesii.*]

SPORNE, K. R. The morphology of gymnosperms. ed. 2. 216 pp. London. 1974.

SQUILLACE, A. E. Analysis of monoterpenes of conifers by gas-liquid chromatography. Pp. 126–157 *in* J. P. MIKSCHE, ed., Modern methods in forest genetics. Berlin. 1976. [Extensive bibliography cross referenced by taxa.]

SRIVASTAVA, L. M. Secondary phloem in the Pinaceae. Univ. Calif. Publ. Bot. **36**: 1–142. 1963. [35 plates of micrographs; compares development and anatomy of species in six genera; emphasis on western North America.]

STAIRS, G. R. Monoterpene composition in *Larix.* Silvae Genet. **17**: 182–184. 1967.

STERLING, C. Structure of the male gametophyte in gymnosperms. Biol. Rev. **38**: 167–203. 1963.

TAYLOR, R. J. The relationship and origin of *Tsuga heterophylla* and *Tsuga Mertensiana* based on phytochemical and morphological interpretations. Am. Jour. Bot. **59**: 149–157. 1972. [Leaf phenolics of *Tsuga* and *Picea* species.]

TEOH, S. B., & H. REES. Nuclear DNA amounts in populations of *Picea* and *Pinus* species. Heredity **36**: 123–137. 1976.

TIEGHAM, P. VAN. Anatomie comparée de la fleur femelle et du fruit des Cycadées, des Conifères et des Gnetacées. Ann. Sci. Nat. Bot. V. **10**: 269–304. 1869. [Important early contribution on ovulate-cone anatomy of the Pinaceae, with emphasis on vasculature.]

––––––. Structure et affinités des *Abies* et des genres les plus voisins. Bull. Soc. Bot. France **38**: 406–415. 1891. [Defines subfamilial groups based on resin-canal position in the primary root; provides synopsis of *Abies* species based on leaf anatomy.]

UENO, J. Some palynological observations of Pinaceae. Jour. Inst. Polytech. Osaka Univ. ser. D. **9**: 163–177. *pls. 1–3.* 1958. [All genera except *Cathaya* compared.]

VIERHAPPER, F. Entwurf eines neuen Systemes der Coniferen. Abh. Zool.-Bot. Ges. Wien **5**(4): 1–56. 1910. [Classification of Pinaceae emphasizing shoot dimorphism.]

VON RUDLOFF, E. Volatile leaf oil analysis in chemosystematic studies of North American conifers. Biochem. Syst. Ecol. **2**: 131–167. 1975a. [Important review paper; includes comparisons of species of *Abies, Tsuga, Pseudotsuga, Picea,* and *Pinus.*]

WANG, F.-H. Life history of *Keteleeria.* I. Strobili, development of the gametophytes and fertilization in *Keteleeria Evelyniana.* Am. Jour. Bot. **35**: 21–27. 1948.

–––––– & T.-S. CHEN. The embryogeny of *Cathaya* (Pinaceae). (In Chinese; English summary.) Acta Bot. Sinica **16**: 64–69. *pls. 1–3.* 1974. [Similar to that of *Pinus.*]

WATTS, W. A. Vegetational history of the eastern United States 25,000 to 10,000 years ago. Pp. 294–310 *in* H. E. WRIGHT, ed., Late-Quaternary environments of the United States. Vol. 1. The Late Pleistocene (S. C. PORTER, ed.). Minneapolis. 1983. [Discusses current vegetation and Quaternary distribution of *Abies, Larix, Picea, Pinus,* and *Tsuga.*]

WILLAMAN, J. J., & B. G. SCHUBERT. Alkaloid-bearing plants and their contained alkaloids. U. S. Dep. Agr. Agr. Res. Serv. Tech. Bull. **1234**. 287 pp. 1961. [See also WILLAMAN, J. J., & H. L. LI, Lloydia **33**(Suppl.). 286 pp. 1970.]

WODEHOUSE, R. P. Pollen grains. xv + 574 pp. New York. 1935. [Pinaceae, 256–268, *fig. 78, pls. 2, 3.*]

ZHOU, B.-N., B.-P. YING, G.-Q. SONG, Z.-X. CHEN, J. HAN, & Y.-F. YAN. Pseudolaric acids from *Pseudolarix Kaempferi.* Pl. Med. **47**: 35–38. 1983. [Structures of antifungal agents from bark of *P. amabilis* (*P. Kaempferi*) characterized.]

KEY TO THE GENERA OF PINACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *monoecious evergreen [or winter-deciduous] trees (rarely shrubs); leaves alternate, linear to acicular, containing resin canals; pollen cones with spirally arranged, flattened microsporophylls; sporophylls with 2 abaxial microsporangia; pollen bisaccate (sometimes nonsaccate); ovulate cones erect or pendent at maturity; bract-scale complexes spirally arranged, flattened; bracts largely free from cone scales, included or exserted; ovules 2 per cone scale, adaxial, with micropyles facing the cone axis; seeds with 1 terminal wing (rarely wingless).*

A. Foliage leaves in fascicles of 2–5, each fascicle subtended by a scale leaf; cone scales thickened at apex, often armed with a prickle. .... 1. *Pinus.*
A. Foliage leaves borne singly, without subtending scale leaves; cone scales not thickened at apex, unarmed.
    B. Twigs roughened by persistent leaf bases (sterigmata); ovulate cones not erect at maturity, falling as a unit.
        C. Leaves squarish in cross section, acute tipped, not abruptly narrowed at base; leading shoot erect. .... 2. *Picea.*
        C. Leaves flattened, blunt tipped, abruptly petiolate at base; leading shoot drooping. .... 3. *Tsuga.*
    B. Twigs not roughened by leaf bases; leaf scars circular, flush with twig; ovulate cones erect at maturity, cone scales shed individually. .... 4. *Abies.*

1. **Pinus** Linnaeus, Sp. Pl. **2**: 1000. 1753; Gen. Pl. ed. 5. 434. 1754.

Evergreen trees (or less commonly shrubs). Bark deeply furrowed to thin and scaly. Wood with axial and radial resin canals and ray tracheids regularly present; axial parenchyma absent. Primary leaves spirally arranged; secondary (foliage) leaves borne in fascicles of 2, 3, or 5 [rarely to 8 or solitary] on highly condensed short-shoots subtended by a scale leaf and surrounded at base by a sheath of bud scales or their remnants; foliage leaves acicular [to linear or rarely lanceolate], entire or minutely serrulate, usually much elongated ([2–]3–50 cm); fibrovascular bundle single (subg. STROBUS) or double (subg. PINUS); resin ducts 2 to several. Pollen cones (microsporangiate strobili) cylindrical, clustered around the bases of the current year's leafy shoots, each borne in the axil of a bract; microsporophylls many per strobilus; microsporangia longitudinally dehiscent; sporophyll apex prolonged into a crest; pollen bisaccate. Ovulate cones terminal or subterminal (sometimes appearing to be lateral) on young lateral shoots, borne singly or more commonly clustered, maturing in the second year [less commonly in the third year, or after ca. 1 year in the tropics]; mature cones usually ovoid to cylindrical, radially symmetrical to oblique, sessile or short stalked, pendulous; bracts much smaller than scales at maturity; ovuliferous scales persistent, obovate to oblong, very woody (or only slightly lignified in some members of subg. STROBUS), with exposed portion (apophysis) thickened and bearing in a terminal or abaxial position the remnant of the exposed portion (umbo) from the first year's development. Seeds with a terminal wing [this sometimes short or absent]; body rounded on the sides and usually acute at base; seed coat hard and somewhat thickened, without resin vesicles. Cotyledons ca. 4–11 [2–18], denticulate or entire. Chromosome number $2n = 24$. (Including *Strobus* Opiz, *Ducampopinus* A. Chev.) LECTOTYPE SPECIES: *P. syl-*

vestris L.; see Britton, N. Am. Trees, 5. 1908. (Classical Latin name for pine.)
— PINE.

Pinus, with approximately 100 species, is the largest genus of conifers and
the most widespread and economically important genus of trees in the Northern
Hemisphere (Critchfield & Little; Mirov, 1967). It occurs from arctic or sub-
arctic areas of North America and Eurasia to subtropical and even tropical
areas of Central America and Asia, with a few species reaching approximately
12°N latitude in the highlands of Nicaragua and Vietnam. The range of one
species, *P. sylvestris* L., extends north of the Arctic Circle in Scandinavia, while
that of *P. Merkusii* Jungh & De Vries crosses the equator in Sumatra. The
greatest number of species (ca. 65) are native to North America, with particular
concentrations in Mexico, California, and the southeastern United States. Thir-
ty-four species are native to Eurasia, with three of these ranging into North
Africa, and one (*P. canariensis* C. Smith) endemic to the Canary Islands. Several
species are now widely grown in the Southern Hemisphere.

The complex history of classification within *Pinus* has been reviewed by
Mirov (1967) and Little & Critchfield. Many of the currently recognized sub-
divisions date to the important 1838 classification of Loudon, which divided
the genus into three sections based on number of needles per fascicle, and then
into 15 groups corresponding to subsections. The division of the genus into
two main groups based on the number of vascular bundles in the needle (one
vs. two), which has been central to most recent classifications, dates to 1893,
when Koehne treated these groups as sections *Haploxylon* and *Diploxylon*
(= subg. STROBUS (D. Don) Lemmon and subg. PINUS, respectively).

Shaw's (1914) worldwide monograph has been the basis from which most
modern classifications of the genus have been developed. He utilized characters
from a diversity of plant parts—including morphology of the shoots, leaves,
ovulate cones, ovuliferous scales, and seeds, and also data on wood anatomy
derived from the research of I. W. Bailey (1910). Shaw's treatment is notable
in emphasizing proposed evolutionary transformation series for seed and cone
characters in the formulation of the classification. Some of the assignments of
character polarity are open to question, and not enough attention was given
to character conflict and the possibility of convergence, but many of his groups
appear to be natural ones. Shaw divided the genus into sections *Haploxylon*
and *Diploxylon,* under which he recognized two subsections each and thirteen
"groups" designated by names and roman numerals. He later (1924) merged
the related white-pine groups *Strobi* and *Flexiles* under the former name. The
yellow pines (subg. PINUS) from our region, along with a diversity of species
from elsewhere in North and Central America and a few from Europe, were
placed in his groups *Australes* and *Insignes,* depending on the degree of serotiny
and cone asymmetry.

More recent treatments, beginning with Pilger's in 1926 and including that
of Little & Critchfield (1969), which is used here, have raised Shaw's infra-
generic groups in rank so that his sections now correspond to subgenera, his
subsections to sections, and his groups to subsections. Later classifications have
diverged most from Shaw in their treatment of groups in subg. PINUS. Duffield's

studies of crossability among species in Shaw's subsect. *Pinaster* (comprising the bulk of subg. PINUS) have resulted in important rearrangements reflected in Little & Critchfield's classification. Further study of the diverse Mexican pine flora has also resulted in the publication of a number of new species in both subg. PINUS (see particularly Martínez, 1948) and subg. STROBUS, where classification of the piñon pines has recently been in great flux (see Eguiluz Piedra, 1988; Zavarin, in press).

Little & Critchfield's classification recognizes three subgenera, PINUS, STROBUS, and DUCAMPOPINUS (A. Chev.) Ferré. The last includes only the unusual Vietnamese *Pinus Krempfii* Lecomte, which has two strongly flattened needles per fascicle but otherwise fits well into subg. STROBUS (see Erdtman *et al.*; Van der Burgh). Little & Critchfield rigorously applied the rules of botanical nomenclature in their choice of names and ranks and utilized information on crossability and, to some degree, chemistry and karyotype in recognizing five sections (essentially the subsections of Shaw plus a new section for *P. Krempfii*) and fifteen subsections, three of which are represented in our area. Another recent classification that strongly emphasizes characters of wood anatomy, along with more traditional morphological characters, is presented in Van der Burgh. It has been modified somewhat by Farjon. Van der Burgh did not split the genus into two main groups representing haploxylon and diploxylon pines but instead implied (see his *fig. 1*) that various groups of diploxylon pines have been derived separately from primitive haploxylon pines (see also Farjon, *fig. 1*, p. 202). He thus divided the genus into eight sections, two among the haploxylon pines and six among the diploxylon pines, and 21 subsections. Many of the sections and subsections are similar to those recognized by Little & Critchfield, but

FIGURE 1. **Pinus** subg. STROBUS sect. STROBUS subsect. STROBUS. a–s, *P. Strobus*: a, tip of shoot with last season's leaves, new growth, and 2 ovulate cones at time of pollination, × ½; b, short-shoots, each showing subtending bract, scale leaves, and 5 developing needle leaves, × 2; c, detail of bases of mature short-shoots, the bracts and scale leaves having abscised, × 2; d, diagrammatic cross section of needle leaf, showing single fibrovascular bundle, endodermis enclosing transfusion tissue, and 2 resin ducts, × 15; e, microsporangiate strobilus (pollen cone) just before sporangial dehiscence, × 4; f, g, lateral and abaxial views of microsporophyll, showing the 2 abaxial sporangia and their dehiscence, × 10; h, pollen grain, showing the 2 saccae, × 250; i, ovulate cone at time of pollination, × 6; j, detail of ovulate cone, showing scales with ovules and subtending bracts, × 10; k, detail in lateral view of single cone scale and subtending bract at time of pollination, 1 ovule with 2 micropylar appendages visible, × 12; l, m, adaxial and abaxial views of cone scale and bract at time of pollination, showing micropylar appendages on the 2 ovules, × 12; n, "whorl" of 4 cones at end of first growing season, all surrounding fascicles of leaves removed, lateral and terminal buds visible, × ½; o, cone scale with 2 developing seeds at time of pollination of the next year's cones, showing remnants of the micropylar appendages and development of wings, × 3; p, mature cone, pendent on tree, seeds already shed, × ½; q, mature seed, after wing has separated from cone scale, × 1; r, longitudinal section of seed, wing removed, showing embryo surrounded by tissue of megagametophyte (stippled), micropyle facing base, × 5; s, embryo, showing suspensor and numerous cotyledons, × 6.

some—particularly in the heterogeneous sections PARRYA Mayr and PINEA Endl.—have been divided more finely. Another quite different classification that emphasizes resin-canal distribution in the needles, cotyledonary formulae (see Ferré, 1953, 1965), and pollen size is given by Gaussen.

Pinus is readily distinguished from the other genera of Pinaceae by its elongate foliage leaves borne in tight clusters of two to five [one to eight] needles on extremely reduced short-shoots, and its distally thickened, woody, often spine-tipped cone scales. As discussed under the family, *Pinus* is linked to the other pinoid genera (*Picea, Cathaya, Larix, Pseudotsuga*) by features of wood and primary root anatomy. *Pinus* shows the greatest overall similarity to *Picea* and *Cathaya,* which are the only other Pinaceae containing serratene triterpenoids. *Pinus* has the longest well-established fossil record of any of the extant genera of Pinaceae, dating back to the Lower Cretaceous. Miller (1976, 1977) has observed that early fossil cones of the Pinaceae are often similar to those of *Pinus* in form and anatomy. This led him to suggest that early evolution of the family was distinctly *Pinus*-centered. Immunological comparisons of seed proteins (Prager *et al.*; Price *et al.*), however, do not provide evidence that *Pinus* diverged before the other nine genera and instead place it within the pinoid group of genera.

The 11 species native to our region fall into two of the subgenera recognized by Little & Critchfield. Subgenus STROBUS (subg. *Haploxylon* (Koehne) Rehder) is characterized by leaves with a single fibrovascular bundle, five needles per fascicle [one to five in sect. PARRYA Mayr] with a deciduous sheath at the base [rarely persistent in sect. PARRYA], and a nondecurrent subtending bract. Members of sect. STROBUS, including the white pines (subsect. STROBUS) and the stone pines (subsect. CEMBRAE Loudon), have five needles per fascicle and cone scales with the umbo terminal and lacking an apical point or bristle.

Subsection STROBUS, which differs from subsect. CEMBRAE in having seed cones that are dehiscent at maturity and winged seeds, comprises 14 species in North and Central America and Eurasia (Little & Critchfield). Our only species, *Pinus Strobus* L. (*Strobus Strobus* (L.) Small), eastern white pine, white pine, $2n = 24$, occurs broadly in the northeastern United States and the Great Lakes states, in southern Canada from extreme southeastern Manitoba to Newfoundland, and south in the Appalachian Mountain region to northern Georgia and South Carolina (Little, 1971, *maps 73N, E*). This species, characteristic of areas with a cool, moist climate, occurs most commonly on well-drained sandy soils, although it also grows on a number of other soil types (Fowells). Huge numbers of these trees were cut for timber in the last two centuries, so few large first-growth individuals, which may reach 40–50 m in height, remain (Peattie). In our area the species occurs up to 1500 m altitude in the Appalachian Mountains of Tennessee, the Carolinas, and Georgia. Disjunct populations are also found in central North Carolina (Chatham and Lee counties; Coker & Totten) and central Tennessee (Cheatham County).

A related taxon from highland areas of southern Mexico and Guatemala has often been treated as *P. Strobus* var. *chiapensis* Martínez (see, for example, Sharp). Andresen (1964, 1966) has treated it as a distinct species, *P. chiapensis* (Martínez) Andresen, on the basis of quantitative studies indicating that the

taxon is less similar to *P. Strobus* than is the western white pine (*P. monticola* Douglas ex D. Don). According to Andresen (1966), *P. chiapensis* differs quantitatively from *P. Strobus* in having longer leaves with a greater number of serrations per unit length, ovulate cones with longer stalks and more scales per cone, and qualitatively in having undulate, truncate cone-scale apices and in lacking recurved cone scales adjacent to the stalk. Chemical comparisons of these taxa will be of great interest in providing independent assessments of relationship.

Subgenus PINUS (subg. *Diploxylon* (Koehne) Rehder, subg. *Eupitys* (Spach) Rehder) (leaves two or three [rarely four to eight] per fascicle, fibrovascular bundles two per needle, basal sheath of fascicle persistent [rarely deciduous], the subtending bract decurrent; seed cones symmetrical or oblique; cone scales with umbo abaxial, often armed with a sharp prickle) comprises at least 62 species (Little & Critchfield) distributed throughout virtually the entire range of the genus. Two subsections of sect. PINUS (seeds with a long [or rarely short] detachable wing, leaf fascicles with a persistent basal sheath) have species native to our area.

Subsection AUSTRALES Loudon (leaves two or three per fascicle, resin ducts internal or medial; seed cones symmetrical, generally opening at maturity; cone scales usually with persistent prickles) comprises 11 species in the eastern United States, the Caribbean islands, and adjacent Central America; eight of them are native to our region. *Pinus palustris* Miller (*P. australis* Michx. f.), longleaf pine, longstraw pine, Georgia pine, yellow pine, $2n = 24$, is found on well-drained sandy soils of the Atlantic and Gulf coastal plains and sometimes up to 600 m altitude on foothills of the adjacent Piedmont, from southeastern Virginia to south-central Florida and west to eastern Texas (Little, 1971, *map 65E*). The species has been heavily exploited for timber and turpentine production, and it has been estimated that by 1930 only ten percent of its original volume of timber remained (Snyder *et al.*). Young trees of *P. palustris* are highly fire tolerant, so the species is often found in pure stands on burned areas.

Pinus palustris is a large tree (to ca. 30 m) with the longest leaves (ca. 25–45 cm) and largest cones (ca. 15–25 cm long) of any pine in the eastern United States. Leaves are three per fascicle, and cones are nonserotinous and have small prickles on the cone scales. The winter buds are distinctively large and whitened. This is one of very few pine species in which the seedlings go through an unusual "grasslike" stage. The stem thickens but elongates very little during the first few years, and the densely overlapping needles protect the growing point (see discussion in Mirov, 1967). This form of seedling development is restricted to a few subtropical or tropical pines and conveys substantial fire resistance.

Natural hybrids between *Pinus palustris* and *P. Taeda* (*P. × Sondereggeri* Chapman) occur with some regularity when the species grow in mixed populations (Snyder *et al.*), but the two species nevertheless remain quite distinct overall. Hybrids of *P. palustris* and *P. Elliottii* var. *Elliottii* occur less frequently in southern Georgia and northern Florida (Mergen, 1958a; Snyder *et al.*).

Pinus Taeda L., loblolly pine, oldfield pine, North Carolina pine, $2n = 24$, is found on the Coastal Plain and Piedmont from southern New Jersey south
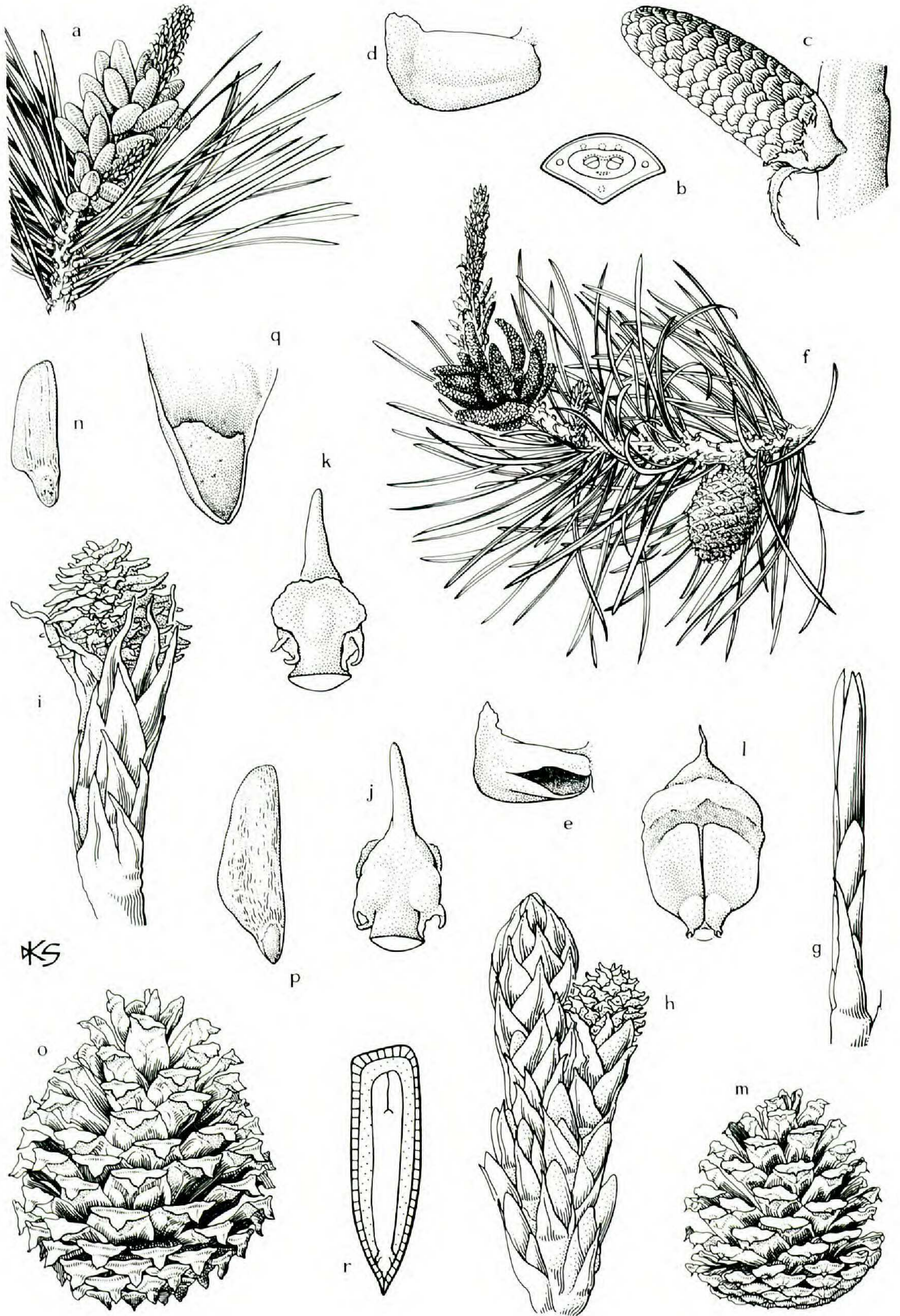
to central Florida and west to southern Arkansas, eastern Texas, and extreme southeastern Oklahoma (Little, 1971, *map 75E*). It is a common tree in South Carolina, Georgia, Alabama, and eastern Mississippi, and north to southern Tennessee. It grows in both poorly drained clay (the name "loblolly" means mud puddle; Little, 1980) and well-drained sandy soil. It rapidly invades abandoned fields on the Coastal Plain, but to a much lesser degree in the Piedmont, where *P. echinata* is the characteristic oldfield pine (Fowells; Little, 1980). Loblolly pine increases in size very rapidly and is the most widely utilized commercial pine in the southeastern United States, being very widely grown in plantations.

Loblolly pine is a large tree (up to 45 m) with stout but relatively flexible needles ca. 15–25 cm long, usually three per fascicle, and cones ca. (5–)7–13 cm long, with short, stout prickles. It differs from the related *Pinus rigida* Miller and *P. serotina* Michx. in having larger, more readily deciduous cones with larger prickles (ca. 2–3 mm long) and wider cone scales (ca. 12–15 vs. 6–10 mm), and nonresinous winter buds (Little *et al.*). In addition to the hybrids with *P. palustris* noted above, *P. Taeda* forms natural hybrids with *P. rigida*, *P. serotina*, and *P. echinata* (Dorman & Zobel; Little *et al.*; Smouse & Saylor, 1973b), but the species remains relatively distinct even in areas of narrow sympatry.

Pinus echinata Miller, shortleaf pine, yellow pine, $2n = 24$, is the most widely distributed of the southern yellow pines, occurring from New Jersey and extreme southeastern New York south to northern Florida and west to eastern

---

FIGURE 2. **Pinus** subg. PINUS sect. PINUS subsect. AUSTRALES. a–n, *P. rigida*: a, tip of shoot with last season's leaves, microsporangiate strobili (pollen cones) before shedding of pollen, and new vegetative lateral and terminal shoots, the fascicles just beginning to expand, the subtending bracts evident, × ½; b, diagrammatic cross section of needle leaf, showing the 2 fibrovascular bundles, nearby sclerenchyma (dotted), and 6 resin canals outside the endodermis, × 15; c, single microsporangiate strobilus and subtending bract before sporangial dehiscence, × 2; d, e, ¾ view of abaxial side of microsporophyll, showing 2 microsporangia, before and after dehiscence, × 10; f, shoot tip after shedding of pollen, showing persistent fascicles, cone of preceding season, new lateral and terminal growth (fascicles only beginning to expand), and microsporangiate strobili just after shedding of pollen, × ½; g, expanding fascicle of 3 foliage leaves with scale leaves and subtending bract (decurrent on stem) below, × 2; h, tip of shoot with terminal bud, lateral shoot with terminal cone (just before pollination), and new fascicles of leaves just beginning to expand, × 2; i, ovulate cone (terminating lateral shoot) at time of pollination, × 3; j, k, adaxial and abaxial views of cone scale with 2 ovules (each with 2 micropylar appendages) and subtending bract at time of pollination, × 12; l, cone scale with 2 developing seeds (from second year's cone in "f") at time of pollination of new cones, showing shriveled micropylar appendages and evident wing of seed, × 3; m, mature cone with seeds shed, × ½; n, seed with wing (abaxial view), × 1. o–r, *P. pungens*: o, mature cone with seeds shed, × ½; p, seed with wing (adaxial view), × 1; q, detail of seed and base of wing (abaxial view), × 3; r, diagrammatic longitudinal section of seed, the seed coat hatched, megagametophyte stippled, embryo (showing 2 cotyledons) unshaded, × 6.

Texas, eastern Oklahoma, Arkansas, and southern Missouri (Little, 1971, *map 52E*). It grows at moderate elevations (to ca. 1000 m) in the Appalachian Mountains and commonly invades abandoned fields on the Piedmont. It is less common on the Coastal Plain (Coker & Totten). The species can grow on many kinds of soils but is best developed on fine sandy loam with good drainage (Fowells). Young plants are capable of surviving repeated fires by sprouting from the root collar (Fowells; Mattoon).

Pinus echinata is a large tree (ca. 20–30 m) with two or occasionally three slender, flexible needles ca.7–13 cm long per fascicle, small (ca. 4–6 cm), conical or narrowly ovoid cones that open at maturity but are long persistent, and cone scales with a small, slender prickle.

Pinus glabra Walter, spruce pine, cedar pine, Walter's pine, $2n = 24$, one of the least common of the southern yellow pines, grows in moist lowland areas of the Coastal Plain from eastern South Carolina south to northern Florida and west to southern Alabama and eastern Louisiana, particularly along river courses (Little, 1971, *map 58E*). It is a large tree (to ca. 30 or more m high) with relatively slender and short needles (ca. 4–10 cm long) in fascicles of two, and small, conical to narrowly ovoid cones (ca. 3–6 cm long) with small, easily shed, slender scale prickles. The characteristic bark is smooth and grayish, in contrast to that of the related *P. echinata,* which is irregularly flaking and reddish brown.

Pinus serotina Michx. f. (*P. rigida* Miller var. *serotina* (Michx. f.) Loudon, *P. rigida* subsp. *serotina* (Michx. f.) R. T. Clausen), pond pine, marsh pine, pocosin pine, $2n = 24$, occurs in somewhat surprising habitats for a pine— sandy swamps and shallow ponds—along the Coastal Plain from southern New Jersey and Delaware south to central and northwestern Florida, often forming nearly pure stands (Little, 1971, *map 74E*). It is a medium-sized tree (generally 10–20 m high) with flexible needles ca. 15–20 cm long and usually three per fascicle. It is characterized by short (ca. 4–6 cm), rounded to ovoid cones that remain unopened on the tree for several years and cone scales that have only a weak prickle. It intergrades morphologically with the closely related *P. rigida,* from which it differs modally in ecology.

Pinus rigida Miller, pitch pine, $2n = 24$, is a small to medium-sized tree that occurs from southern Maine and extreme southern Quebec and Ontario through New England and the mid-Atlantic states and south, mostly in the Appalachian Mountains, to northern Georgia and South Carolina. It is tolerant of dry, rocky soils but also occurs on sands and sometimes in swampy soils. The needles are usually three per fascicle, stout, and ca. 7–13 cm long; the cones are ovoid, 3–7 cm long, long persistent, occasionally serotinous, and generally with sharp, slender prickles. Pitch pine is highly resistant to fire and other forms of injury and sprouts from roots and stumps after damage, becoming very irregular in form (Ledig & Fryer, 1974; Little, 1980). Dwarfed plants of the species are characteristic of parts of the Pine Barrens of New Jersey, where the high incidence of fire may have selected for cone serotiny, a feature otherwise not typical of the species (Givnish; Ledig & Fryer, 1972).

A number of authors have discussed the geographic variation of *Pinus rigida* in relation to that of *P. serotina,* with which it intergrades in New Jersey,

Delaware, and Maryland (Clausen; Ledig & Fryer, 1974; Smouse & Saylor, 1973a, b). The two are largely allopatric and differ modally in ecology and morphology but show clinal variation in a number of characters. Smouse & Saylor (1973a, b) found pond and pitch pines to group much more closely in multivariate analyses than loblolly and shortleaf pines did (all of these taxa being subject to natural hybridization) and suggested that *P. serotina* should be treated as a subspecies of *P. rigida.* Other recent authors (Ledig & Fryer, 1974; Little, 1980) have continued to treat them at the level of species.

Pinus pungens Lamb., Table Mountain pine, prickly pine, hickory pine, $2n = 24$, is a small to medium-sized tree of the Appalachian area from southeastern Pennsylvania south to extreme northeastern Georgia and eastern Tennessee, and also locally in New Jersey, Delaware, and the District of Columbia (Little, 1971, *map 66E*). In our area the species occurs on dry, rocky slopes and ridges of the Appalachians up to ca. 1200 m altitude. The species has two stiff, usually twisted needles per fascicle and ovoid, long-persistent cones that differ from those of the other eastern pines in their very stout, incurved prickles. The cones are at least sometimes serotinous (C. E. Wood, pers. comm.). *Pinus pungens* is named "hickory pine" because of its tough, hickorylike branches.

Pinus Elliottii Engelm. (*P. caribaea* sensu Small, non Morelet; *P. palustris* sensu Small, non Miller; *P. heterophylla* (Ell.) Sudw., 1893, non K. Koch, 1849), slash pine, swamp pine, $2n = 24$, occurs along the Coastal Plain from central South Carolina to southern Florida and west to southern Mississippi and eastern Louisiana. It is also naturalized in eastern Texas. Little & Dorman (1952b, 1954) distinguished two geographic varieties: var. *densa* Little & Dorman, of central and southern Florida, differs from var. *Elliottii* in having a grasslike seedling stage and a lower average number of needles per fascicle. Rangewide geographic variation in morphological and physiological traits was thoroughly examined by Squillace (1966), who used both field and common orchard studies. There are significant differences between the varieties in the means of several characters, but the patterns of variation are largely continuous within and between them, and there is no increase in variability in the area of transition in central Florida. Variety *Elliottii* was originally largely confined to ponds, pond margins, and other poorly drained habitats (Fowells), but it has become more widespread in its range because natural fires have been suppressed. South Florida slash pine (var. *densa*) occurs in dryish flatwoods and on thin soil over limestone (Hardin; Squillace, 1966). Because of its thicker stems and better protected growing points in young plants, it shows a greater degree of fire tolerance than does var. *Elliottii* (Squillace, 1966).

Pinus Elliottii is a medium-sized to large tree (to 30 m or more) with stout, stiff needles ca. 15–30 cm long, both two and three per fascicle, and narrowly ovoid cones ca. 6–15(–18) cm long with relatively short prickles. It is closely related to *P. caribaea* Morelet, of the Caribbean Islands and Central America, under which it was formerly treated, but differs in having longer (1–2 vs. < 1 mm) cone-scale prickles, broader seeds with more readily detachable wings, and needles in fascicles of two and three, rather than consistently three or more (Little & Dorman, 1954). *Pinus Elliottii* can be crossed artificially with several species including *P. caribaea* in subsect. AUSTRALES, and also with *P. clausa*

in subsect. CONTORTAE (Critchfield, 1963; Saylor & Koenig), but under natural conditions it hybridizes only occasionally with *P. palustris* (Mergen, 1958a).

Subsection CONTORTAE Little & Critchfield (leaves two per fascicle, short (2–8 cm), often twisted, with mostly medial resin ducts; seed cones small (3–8 cm long), symmetrical [or oblique], often serotinous, long persistent; cone scales with [or without] a persistent prickle) is quite similar in morphology to subsect. AUSTRALES, and the two subsections may be more appropriately combined once their evolutionary relationships are better understood. Subsection CONTORTAE comprises four species native to the United States and Canada, of which two, *P. clausa* (Engelm.) Vasey ex Sarg. and *P. virginiana* Miller, are native in our region. A third species, *P. Banksiana* Lamb., jack pine, which now has a native range north of our region in Canada and the Great Lakes states, occurred in parts of the southeastern United States during the Late Pleistocene (Watts, 1970, 1980).

Pinus clausa, sand pine, scrub pine, spruce pine, $2n = 24$, occurs on well-drained sandy soils from extreme southwestern Alabama east through the panhandle of northwestern Florida, as well as in scattered localities through much of peninsular Florida, except in the extreme south (Little, 1971; Ward, 1963). It often forms dense pure stands and is the dominant tree in some 200,000 acres in Marion Co., Florida (Ward, 1963). Two geographic races have been defined: the Ocala race (var. *clausa*), with serotinous cones, including almost all of the peninsular populations, and the Choctawhatchee race (var. *immuginata* Ward), with cones opening at maturity, encompassing most of the northwestern populations (Little & Dorman, 1952a; Ward, 1963; Wheeler *et al.*). The two cone morphs occur intermixed in several areas of northwestern Florida (Ward, 1963), and no other obvious morphological differences are present, so formal designation as varieties seems unwarranted.

The closely related *Pinus virginiana* Miller, Virginia pine, scrub pine, poverty pine, Jersey pine, $2n = 24$, geographically separated by over 100 km from *P. clausa,* occupies a broad area from Long Island and New Jersey west to Ohio and southern Indiana and south to northern South Carolina and Georgia, central and northern Alabama, and northeastern Mississippi (Little, 1971, *map 77E*). In our region it is found primarily in the Piedmont and at moderate elevations (usually below 1000 m) in the Appalachians. It occurs very occasionally on the Coastal Plain in the Carolinas and Georgia (Coker & Totten). Tending to grow on dry, shallow soils, including clay, loam, or (less commonly) sandy soils near the coast, it often invades old fields on the Piedmont as a pioneer species (Kellison & Zobel). It is a medium-sized tree with relatively short (ca. 4–8 mm), stout needles and narrowly ovate, persistent but nonserotinous cones. It differs from *P. clausa* primarily in having longer (ca. 5 mm), more slender cone-scale prickles, and stouter, more often twisted needles (Coker & Totten; Little, 1980), as well as in its edaphic tolerances.

Pinus virginiana is very similar in isozyme profiles to *P. clausa* (Wheeler *et al.*), with which it is readily crossable (Critchfield, 1963; Kellison & Zobel). Both show strong cross-incompatibility with the two remaining species of subsect. CONTORTAE (*P. contorta* Douglas ex Loudon and *P. Banksiana*). The electrophoretic evidence is consistent with the hypothesis that *P. virginiana* is

a relatively recent derivative of an ancestor similar to *P. clausa,* and Wheeler *et al.* have suggested that the two taxa be treated as ecogeographic subspecies. Preliminary data on turpentine composition (Mirov, 1961) indicating differences in terpenoid profiles between these species need further confirmation.

Chromosome numbers have been reported for approximately 90 species of *Pinus*; with the exception of occasional aberrant individuals, all have $2n = 24$ (see particularly Khoshoo, 1961; Santamour, 1960; Sax & Sax; Saylor, 1964, 1972, 1983; Styles & Khosla). Karyotypes have been reported for 87 species in the systematic surveys of Saylor (1964, 1972, 1983), and chromosome constriction patterns have been examined in detail by Pederick for a much smaller sample of species. The smallest chromosome is definitely heterobrachial (with a submedian centromere) in *Pinus,* while the other 11 are approximately isobrachial, except in subsect. PINUS (subsect. *Sylvestres* of Saylor, 1972), in which the second smallest chromosome is also somewhat heterobrachial. Patterns of arm lengths and arm-length ratios are reasonably concordant with the Little & Critchfield classification of subg. PINUS and lend some support to the separation of the southern yellow pines into subsects. AUSTRALES and CONTORTAE. Patterns are more variable within some subsections in subg. STROBUS, particularly among the white and stone pines of sect. STROBUS.

As noted in the species discussions above, natural hybridization occurs between a number of species of pines within the subsections recognized by Little & Critchfield. In many cases, however, interspecific hybridization is greatly restricted or prevented by a combination of phenological and physiological barriers (see discussions in Critchfield, 1963, and Mirov, 1967). Natural hybrids between species in closely related subsections occur only infrequently (Mirov, 1967)—for example, between *Pinus Coulteri* D. Don and *P. Jeffreyi* Grev. & Balf. (Zobel). Zones of hybridization between certain species—for example, *P. Banksiana* and *P. contorta* in western Canada (Dancik & Yeh; Mirov, 1956b; Moss; Wagner *et al.*; Zavarin *et al.,* 1969)—have been studied intensively through a number of biochemical techniques, as well as morphological comparisons.

Thorough investigations (see particularly Critchfield, 1963, 1966, 1967, 1977, 1986; Duffield) of artificial crossability among pine species have had a major impact on the systematics of the genus. These results have been particularly important in evaluating relationships among the diploxylon pines (see Critchfield, 1963; Duffield; Little & Critchfield) and have led to the treatment of the southern yellow pines under subsections AUSTRALES and CONTORTAE, rather than intermixed with the western North American closed-cone pines of subsect. OöCARPAE Little & Critchfield as in the classifications of Shaw (1914) and Pilger (1926). The species in subsect. AUSTRALES are all linked directly or indirectly by successful crosses (Critchfield, 1963), although some individual combinations (e.g., *P. palustris* × *P. echinata*) seem to be highly cross-incompatible. Crossability within a number of other subsections (e.g., among the pines in sect. STROBUS; Critchfield, 1986) is much more restricted and may sometimes show unpredictable geographic patterns. No successful crosses between species representing different subgenera have ever been made.

Pinus is notable for the great diversity in the size of its cones and the form

of its cone scales (Sargent, 1897; Shaw, 1914). The morphological complexity of the cone-scale apex relates directly to the multi-year development of the ovulate cone, with the areas left exposed in the first-year conelet (the umbo) and in the mature cone (the apophysis) both being evident. The extremely stout prickles seen in several species of subg. PINUS (e.g., *P. pungens* and *P. Sabiniana* Douglas ex D. Don) presumably act as a deterrent to seed predation (McCune).

Klaus (1980), who has surveyed cone-scale form and ornamentation in relation to the systematics of *Pinus,* emphasized the central position of sect. PARRYA in the evolution of the genus. This section of subg. STROBUS (which includes the lacebark, bristlecone, and piñon pines) has an abaxial ("dorsal") umbo, often with an apical point or bristle, and thus provides a morphological link with subg. PINUS, which invariably has an abaxial umbo. The same pattern of relationship is seen in wood anatomy (Hudson; Van der Burgh). The amount of toothing on the walls of the ray tracheids is greater in subg. PINUS than in sect. STROBUS, while the species of sect. PARRYA span most of the range in denticulation of the genus. Other types of characters separate the haploxylon (subg. STROBUS) and diploxylon (subg. PINUS) pines more sharply. Pollen grains of species in subg. STROBUS have a strongly ornamented germinal zone, while those of species in subg. PINUS have a relatively smooth one (Sivak). The profiles of heartwood phenolic compounds (H. Erdtman, 1959; Norin), discussed below, also separate the haploxylon pines (including *P. Krempfii*) from the diploxylon ones.

Pinus shows great diversity in seed size and in the degree of seed winging. Loss of a seed wing in the stone pines (subsect. CEMBRAE) and the piñon pines (subsect. CEMBROIDES) is part of a morphological syndrome related to seed dispersal by corvid birds, especially jays and nutcrackers, or to a lesser degree by rodents (Lanner, 1982; McCune).

Cone serotiny occurs in a number of North American species in subg. PINUS (particularly in subsects. CONTORTAE and OÖCARPAE, but also in a few species of subsects. AUSTRALES and SABINIANAE Loudon (McCune; Mirov, 1967)). Many such species are polymorphic for serotiny, so some seed dispersal can occur in the absence of major fires (McCune). A simple genetic basis for polymorphism in this character has been demonstrated in some species (Sittmann & Tyson). Many of the serotinous species have asymmetric cones, a character that may have been overemphasized in Shaw's (1914) classification, given its potential for convergence.

Mirov (1958, 1961) did a preliminary survey of turpentine composition for the majority of species of *Pinus.* Most species have a steam-distillable oleoresin fraction composed predominantly of various monoterpenoids, but in some it is made up almost entirely of hydrocarbons such as n-heptane. Turpentine composition does not separate major groups such as subgenera but is often valuable in the determination of interspecific hybrids, since closely related species (e.g., *P. Banksiana* and *P. contorta* in subsect. CONTORTAE) may differ considerably in their profiles. Leaf-oil composition is reviewed for a number of North American species by Von Rudloff, and wood or leaf oleoresins have been studied for a number of groups in subg. STROBUS by Zavarin and coworkers (see, for example, Zavarin *et al.* (1982) on subsect. BALFOURIANAE, and Zavarin (in press) and Zavarin & Snajberk (1980, 1987) on subsect. CEMBROIDES).

The composition of heartwood phenolics has been surveyed for over 80 species of *Pinus* and has proved to be very useful in distinguishing the haploxylon and diploxylon pines (H. Erdtman, 1959, 1963; Norin). Members of subg. PINUS have a characteristic, relatively simple pattern that includes the stilbene compound pinosylvin and its methyl ethers and the flavanone derivatives pinocembrin and pinobanksin. The members of subg. STROBUS also have these compounds, as well as dihydropinosylvin and various flavone derivatives. Some groups within subg. STROBUS also contain C-methylated flavonoids. It is postulated that the enzymatic capabilities needed to produce these additional groups of compounds have been lost in the common ancestor(s) of subg. PINUS (H. Erdtman, 1959; Norin). *Pinus Krempfii,* although treated as a separate subgenus by Little & Critchfield, has a pattern of compounds characteristic of subg. STROBUS (Erdtman *et al.*).

Results of allozyme or isozyme electrophoresis have been used in systematic or evolutionary studies in several species groups of *Pinus* (e.g., Conkle *et al.* on the *P. brutia–P. halepensis* complex; Millar *et al.* on the California members of subsect. OÖCARPAE; Steinhoff *et al.* on *P. monticola*; Wheeler *et al.* on subsect. CONTORTAE), and a number of similar studies are now in progress. Levels of within-population variation for electrophoretic alleles are generally high in pines and other long-lived, wind-pollinated trees (Hamrick *et al.*), but they are extremely low in some species—for example, *P. resinosa* Aiton (Fowler & Morris) and *P. Torreyana* Parry (Ledig & Conkle).

Pines are of exceptional economic importance for their timber, which is used for construction, pulpwood, and numerous other purposes. Among the eastern North American species, *Pinus Elliottii, P. palustris,* and *P. Strobus* yield particularly high quality lumber for construction, although *P. Taeda* is now more widely available. The rapid-growing *Pinus radiata* D. Don (a narrow endemic in coastal California and nearby islands) is now one of the most widely cultivated timber trees in the Southern Hemisphere. Several species (e.g., *P. echinata, P. Elliottii,* and *P. palustris* in our area) are tapped for stem oleoresin, from which commercial turpentine, tar oils, rosin, and pitch are obtained by distillation (Dallimore & Jackson; Mirov, 1961, 1967). Pine-leaf oil, utilized medicinally, is also obtained from various species by distillation. Highly esteemed edible seeds (pine nuts) are obtained from large-seeded species (e.g., *P. Pinea* L., umbrella pine; *P. edulis* Engelm., piñon; and *P. Gerardiana* Wallich) in Mediterranean Europe, North America, and Asia. Many species are of horticultural importance, and several are prized for bonsai.

REFERENCES:

Under family references see I. W. BAILEY; L. H. BAILEY; BEAN; BOUREAU; BUCHHOLZ, 1920, 1931; BUTTS & BUCHHOLZ; CAMPO & SIVAK; CAMPO-DUPLAN; CARRIÈRE; CHANG; C. R. CHOWDHURY, 1962; COKER & TOTTEN; CRITCHFIELD; DALLIMORE & JACKSON; DOYLE, 1945, 1963; DOYLE & BRENNAN; G. ERDTMAN, 1957, 1965; H. ERDTMAN, 1959, 1963; FERRÉ; FLORIN, 1931, 1951, 1963; FLOUS; FOWELLS; GAUSSEN, 1960; GREGUSS, 1955, 1972; HAMRICK *et al.*; HARDIN; HEGNAUER, 1962, 1986; HICKEL; HUNTLEY & BIRKS; KHOSHOO, 1961; KRÜSSMANN; LITTLE, 1971, 1980; MILLER, 1976, 1977, 1985; NORIN; OWENS & SIMPSON; PHILLIPS; PILGER; PRAGER *et al.*; PRICE *et al.*; RADAIS; REHDER, 1940, 1949; SANTAMOUR, 1960, 1966; SARGENT, 1897; SAX & SAX; SINGH; SIVAK; SQUILLACE; TEOH & REES; UENO; VON RUDLOFF; and WATTS.

The literature on *Pinus* is very extensive, particularly with regard to chemistry, ecology, economic uses, genetics, and silviculture. The selected references below are weighted toward broad-based systematic studies, review papers, and studies on the species of our region. MIROV (1967) provides a useful compilation of references on the genus up to the mid 1960's.

ABBE, L. B., & A. S. CRAFTS. Phloem of white pine and other coniferous species. Bot. Gaz. **100:** 695–722. 1939.

ALLEN, R., & A. B. WARDROP. The opening and shedding mechanism of the female cones of *Pinus radiata.* Austral. Jour. Bot. **12:** 125–134. *pls. 1–8.* 1964. [See also HARLOW *et al.*]

ANDRESEN, J. W. The taxonomic status of *Pinus chiapensis.* Phytologia **10:** 417–421. 1964. [Treated as distinct from *P. Strobus.*]

————. A multivariate analysis of the *Pinus chiapensis–monticola–Strobus* phylad. Rhodora **68:** 1–24. 1966.

ANDREWS, E. F. Agency of fire in propagation of longleaf pines. Bot. Gaz. **64:** 497–508. 1917. [Dense covering of needles protects the growing point of young plants from fire.]

AXELROD, D. I. History of the maritime closed-cone pines, Alta and Baja California. Univ. Calif. Publ. Geol. Sci. **120.** x + 144 pp. 1980. [History of subsect. OÖCARPAE as inferred from fossil material.]

————. Cenozoic history of some western American pines. Ann. Missouri Bot. Gard. **73:** 565–641. 1986. [Distribution maps; photographs of ovulate cones of extant and extinct (fossil) species.]

BAILEY, D. K. Phytogeography and taxonomy of *Pinus* subsection *Balfourianae.* Ann. Missouri Bot. Gard. **57:** 210–249. 1970. [*P. longaeva* separated from *P. aristata.*]

————. A study of *Pinus* subsection *Cembroides* I: The single-needle pinyons of the Californias and the Great Basin. Notes Roy. Bot. Gard. Edinburgh **44:** 275–310. 1987. [Proposes a new species, *P. californiarum.*]

BAILEY, I. W. Anatomical characters in the evolution of *Pinus.* Am. Nat. **44:** 284–293. 1910.

BARNETT, J. P., & B. F. McLEMORE. Cone and seed characteristics of sand pine. U. S. Dep. Agr. Forest Serv. Res. Pap. **SD-19.** 13 pp. 1965. [Reports responses of cones of *P. clausa* to heating.]

BUCHHOLZ, J. T. Suspensor and early embryo of *Pinus.* Bot. Gaz. **66:** 185–228. *pls. 6–10.* 1918.

————. Embryological aspects of hybrid vigor in pines. Science **102:** 135–142. 1945.

CHAPMAN, H. H. The place of fire in the ecology of pines. Bartonia **26:** 39–44. 1952. [Reviews response to fire of eastern North American species, including six from our region.]

CLAUSEN, R. T. Contributions to the flora of New Jersey. Torreya **39:** 125–133. 1939. [*Pinus serotina* treated as a subspecies of *P. rigida.*]

CONKLE, M. T., G. SCHILLER, & C. GRUNWALD. Electrophoretic analysis of diversity and phylogeny of *Pinus brutia* and closely related taxa. Syst. Bot. **13:** 411–424. 1988.

CÔTÉ, W. A., & A. C. DAY. Wood ultrastructure of the southern yellow pines. Syracuse Univ. Coll. Forestry Tech. Publ. **95.** 70 pp. 1969. [Extensive SEM comparisons of ten species; few consistent differences observed.]

CRITCHFIELD, W. B. Geographic variation in *Pinus contorta.* Maria Moors Cabot Found. Publ. **3:** 1–118. 1957.

————. Hybridization of the southern pines in California. Southern Forest Tree Improvement Comm. Publ. **22:** 1–9. 1963. [Crossability among the species of subg. PINUS from the southeastern United States.]

————. Crossability and relationships of the California bigcone pines. U. S. Dep. Agr.

Forest Serv. Res. Pap. **NC-6:** 36–44. 1966. [*P. Coulteri, P. Jeffreyi, P. Sabiniana.*]

———. Crossability and relationships of the closed-cone pines. Silvae Genet. **16:** 89–97. 1967. [Relationships within subsect. Oöcarpae.]

———. Hybridization of foxtail and bristlecone pines. Madroño **24:** 193–212. 1977. [*P. aristata, P. Balfouriana, P. longaeva.*]

———. Crossability and relationships of Washoe pine. *Ibid.* **31:** 144–170. 1984. [*P. washoensis.*]

———. The late Quaternary history of lodgepole and jack pines. Canad. Jour. Forest Res. **15:** 749–772. 1985. [*P. contorta, P. Banksiana.*]

———. Hybridization and classification of the white pines (*Pinus* section *Strobus*). Taxon **35:** 647–656. 1986.

——— & B. B. KINLOCK. Sugar pine and its hybrids. Silvae Genet. **35:** 138–145. 1986. [*P. Lambertiana.*]

——— & E. L. LITTLE, JR. Geographic distribution of the pines of the world. U. S. Dep. Agr. Forest Serv. Misc. Publ. **999:** 1–97. 1966. [Excellent maps of all species then known; treatment using the new classification detailed by LITTLE & CRITCHFIELD.]

DALLIMORE, W. The yellow pines of North America. Bull. Misc. Inf. Kew **1921:** 330–335. 1921.

DANCIK, B. P., & F. C. YEH. Allozyme variability and evolution of lodgepole pine (*Pinus contorta* var. *latifolia*) and jack pine (*P. Banksiana*) in Alberta. Canad. Jour. Genet. Cytol. **25:** 57–64. 1983.

DE LAUBENFELS, D. J. Coniferales. Fl. Malesiana. ser. 1. **10**(3): 337–453. 1988. [Pinaceae, 447–453; *P. Merkusii, P. kesiya* Royle ex Gordon.]

DEVALL, W. B. The taxonomic status of *Pinus caribaea* Mor. Proc. Florida Acad. Sci. **5:** 121–132. 1941. [Comparisons of *P. palustris* and *P. Elliottii* (under *P. caribaea*).]

DOAK, C. C. Evolution of foliar types, dwarf shoots, and cone scales of *Pinus,* with remarks concerning similar structures in related forms. Illinois Biol. Monogr. **13:** 1–106. 1935.

DORMAN, K. W., & A. E. SQUILLACE. Genetics of slash pine. U. S. Dep. Agr. Forest Serv. Res. Pap. **WO-20.** 20 pp. 1974. [*P. Elliottii.*]

——— & B. J. ZOBEL. Genetics of loblolly pine. U. S. Dep. Agr. Forest Serv. Res. Pap. **WO-19.** 21 pp. 1973. [*P. Taeda.*]

DOYLE, J., & M. O'LEARY. Pollination in *Pinus.* Sci. Proc. Roy. Dublin Soc. **21:** 181–190. *pl. 3.* 1935.

DUFFIELD, J. W. Relationships and species hybridization in the genus *Pinus.* Silvae Genet. **1:** 93–97. 1952. [Results of an extensive program of artificial hybridization with emphasis on subg. PINUS.]

EGUILUZ PIEDRA, T. Geographic variation in needles, cones and seeds of *Pinus Tecunumanii* in Guatemala. Silvae Genet. **33:** 72–79. 1984.

———. Distribución natural de los pinos en México. Notas Técn. Centro Genét. Forest. Chapingo **1:** 1–6. 1988. [Includes 52 species.]

ENGELMANN, G. Revision of the genus *Pinus,* and description of *Pinus Elliottii.* Trans. Acad. St. Louis **4:** 161–189. 1880. [Treats the species under two sections and eight subsections.]

ERDTMAN, H., B. KIMLAND, & T. NORIN. Wood constituents of *Ducampopinus Krempfii* (Lecomte) Chevalier (*Pinus Krempfii* Lecomte). Phytochemistry **5:** 927–931. 1966. [*P. Krempfii* shows pattern of heartwood phenolics typical of subg. STROBUS.]

EWERS, F. W., & R. SCHMID. Longevity of needle fascicles of *Pinus longaeva* (bristlecone pine) and other North American pines. Oecologia **51:** 107–115. 1981.

FARJON, A. Pines: drawings and descriptions of the genus *Pinus.* 220 pp. Leiden. 1984. [Illustrations; coarse-scale maps; classification and tables of morphological data modified from VAN DER BURGH, with discussion of phylogeny by VAN DER BURGH and schematic evolutionary diagrams by FARJON.]

FERGUSON, M. C. Contributions to the knowledge of the life history of *Pinus* with special reference to sporogenesis, the development of the gametophytes and fertilization. Proc. Wash. Acad. Sci. **6:** 1–202. *pls. 1–24.* 1904. [Data primarily from *P. Strobus.*]

FERNALD, M. L. The confused bases of the name *Pinus palustris.* Rhodora **50:** 241–249. 1948. [Proposes that *P. australis* Michx. be applied; see WARD, 1974, for counterarguments.]

FERRÉ, Y. DE. Quelques particularités anatomiques d'un pin indochinois: *P. Krempfii.* Trav. Lab. Forest. Toulouse, Tome I, Vol. IV, Art. XXV: 1–6. *figs. 1–4.* 1948.

————. Division du genre *Pinus* en quatre sous-genres. Compt. Rend. Acad. Sci. Paris **236:** 226–228. 1953.

————. Structure des plantules et systématique du genre *Pinus.* Bull. Soc. Hist. Nat. Toulouse **100:** 230–280. 1965. [Types of cotyledons, based on arrangement of vascular bundles; data on cotyledon numbers independent of those in BUTTS & BUCHHOLZ; reprinted in Trav. Lab. Forest. Toulouse, Tome II, Sect. I, Vol. II, Art. II: 1–50. 1965.]

FLORENCE, L. Z., & R. R. HICKS, JR. Further evidence for introgression of *Pinus Taeda* with *Pinus echinata*: electrophoretic variability and variation in resistance to *Cronartium fusiforme.* Silvae Genet. **29:** 41–43. 1980. [Disc electrophoresis with general protein staining.]

FOWLER, D. P. Effects of inbreeding in red pine, *Pinus resinosa* Ait. Silvae Genet. **13:** 170–177. 1964. [Effects are limited due to high homozygosity; see also *Ibid.* **14:** 12–23, 37–46. 1965.]

———— & R. W. MORRIS. Genetic diversity in red pine: evidence for low genic heterozygosity. Canad. Jour. Forest Res. **7:** 343–347. 1977. [No detectable electrophoretic variation; variation for null alleles has been reported by F. W. ALLENDORF, K. L. KNUDSEN, & G. M. BLAKE (Genetics **100:** 497–504. 1982).]

FURNIER, G. R., & W. T. ADAMS. Geographic patterns of allozyme variation in Jeffrey pine. Am. Jour. Bot. **73:** 1009–1115. 1986. [*P. Jeffreyi.*]

GIVNISH, T. H. Serotiny, geography, and fire in the Pine Barrens of New Jersey. Evolution **35:** 101–112. 1981. [Factors affecting frequency of serotiny in *Pinus rigida*; see also LEDIG & FRYER, 1972.]

GREENWOOD, M. S. Gene exchange in loblolly pine: the relation between pollination mechanisms, female receptivity and pollen viability. Am. Jour. Bot. **73:** 1443–1451. 1986.

GRIERSON, A. J. C., D. G. LONG, & C. N. PAGE. Notes relating to the flora of Bhutan: III. *Pinus bhutanica*: a new 5-needle pine from Bhutan and India. Notes Roy. Bot. Gard. Edinburgh **38:** 297–310. 1980.

GRIFFIN, J. R. Cone morphology in *Pinus Sabiniana.* Jour. Arnold Arb. **45:** 260–273. 1964.

GURIES, R. P., & F. T. LEDIG. Genetic diversity and population structure in pitch pine (*Pinus rigida* Mill.). Evolution **36:** 387–402. 1982.

HALLER, J. R. Variation and hybridization in ponderosa and Jeffrey pines. Univ. Calif. Publ. Bot. **34:** 123–166. 1962.

HARLOW, W. M. The identification of the pines of the United States, native and introduced, by needle structure. New York State Coll. Forestry Tech. Publ. **32:** 1–21. *pls. 1–19.* 1931. [Extensive illustrations of cross-sectional anatomy.]

————, W. A. CÔTÉ, JR., & A. C. DAY. The opening mechanism of pine cone scales. Jour. Forestry **62:** 538–540. 1964.

HAUPT, A. W. Oögenesis and fertilization in *Pinus Lambertiana* and *P. monophylla.* Bot. Gaz. **102:** 482–498. 1941.

HERBIN, G. A., & K. SHARMA. Studies on plant cuticular waxes. V. The wax coatings of pine needles: a taxonomic survey. Phytochemistry **8:** 151–160. 1969.

HUDSON, R. H. The anatomy of the genus *Pinus* in relation to its classification. Jour. Inst. Wood Sci. **6:** 26–46. 1960. [Comparative wood anatomy.]

JÄHRIG, M. Beiträge zur Nadelanatomie und Taxonomie der Gattung *Pinus* L. Willdenowia **3**: 329–366. 1962. [New classification based on needle anatomy; agrees poorly with those based on other characters.]

JEFFREY, E. C. On the structure of the leaf in Cretaceous pines. Ann. Bot. **22**: 207–220. *pls. 13, 14.* 1908.

KELLISON, R. C., & B. J. ZOBEL. Genetics of Virginia pine. U. S. Dep. Agr. Forest Serv. Res. Pap. **WO-21**. 10 pp. 1973. [*P. virginiana.*]

KENG, H., & E. L. LITTLE, JR. Needle characteristics of hybrid pines. Silvae Genet. **10**: 131–146. 1961. [Detailed descriptions and anatomical illustrations for 42 interspecific hybrids in *Pinus.*]

KLAUS, W. Saccusdifferenzierungen an Pollenkörnern ostalpiner *Pinus*-Arten. Österr. Bot. Zeitschr. **120**: 93–116. 1972.

————. On the taxonomic significance of tectum sculpture characters in alpine *Pinus* species. Grana **17**: 161–166. 1978.

————. Neue Beobachtungen zur Morphologie des Zapfens von *Pinus* und ihre Bedeutung für die Systematik, Fossilbestimmung, Arealgestaltung und Evolution der Gattung. Pl. Syst. Evol. **134**: 137–171. 1980. [Relationships based on umbo and mucro characters of the cone scales.]

KOEHNE, E. Deutsche Dendrologie. 601 pp. Stuttgart. 1893. [Proposes sections *Haploxylon* and *Diploxylon.*]

KONAR, R. N. The morphology and embryology of *Pinus Roxburghii* Sar. with a comparison with *Pinus Wallichiana* Jack. Phytomorphology **10**: 305–319. 1960.

———— & S. RAMCHANDANI. The morphology and embryology of *Pinus Wallichiana* Jack. Phytomorphology **8**: 328–346. 1958.

KONDRATYUK, E. M. An attempt to utilize the characteristics of pollen for classification of pine tree species. (In Ukrainian.) Visn. Akad. Nauk Ukrajins'k. RSR Bot. Sad. **3**: 25–27. 1961.*

KRUGMAN, S. L. The leuco-anthocyanin distribution in the genus *Pinus.* Forest Sci. **5**: 169–173. 1959. [Ubiquitous in leaf, wood, and bark samples of the genus.]

LANGLET, O. A cline or not a cline—a question of Scots pine. Silvae Genet. **8**: 13–22. 1959. [*P. sylvestris.*]

LANNER, R. M. Natural hybridization between *Pinus edulis* and *Pinus monophylla* in the American Southwest. Silvae Genet. **23**: 108–116. 1974. [See also D. K. BAILEY, 1987.]

————. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canad. Jour. Forest Res. **12**: 391–402. 1982. [Discusses loss of seed wing and cone opening mechanism in *P. albicaulis.*]

LECOMTE, H. Un pin remarquable de l'Annam. Bull. Mus. Hist. Nat. Paris **2**: 193–197. 1921. [*P. Krempfii.*]

LEDIG, F. T., & M. T. CONKLE. Gene diversity and genetic structure in a narrow endemic, Torrey pine (*Pinus Torreyana* Parry ex Carr.). Evolution **37**: 79–85. 1983. [Exhibits very low diversity in electrophoretic alleles.]

———— & J. H. FRYER. A pocket of variability in *Pinus rigida.* Evolution **26**: 259–266. 1972. [Geographic variation in frequency of cone serotiny.]

———— & ————. Genetics of pitch pine. U. S. Dep. Agr. Forest Serv. Res. Pap. **WO-27**. 14 pp. 1974. [*P. rigida.*]

LITTLE, E. L., JR. Key to Mexican species of pines. Carib. Forester **23**: 72–77. 1962.

———— & W. B. CRITCHFIELD. Subdivisions of the genus *Pinus* (pines). U. S. Dep. Agr. Forest Serv. Misc. Publ. **1144**: 1–51. 1969. [Reviews previous classifications and presents a new synthetic classification.]

———— & K. W. DORMAN. Geographic differences in cone-opening in sand pine. Jour. Forestry **50**: 204, 205. 1952a. [Two races of *P. clausa* distinguished by presence or absence of serotiny.]

———— & ————. Slash pine (*Pinus Elliottii*), its nomenclature and varieties. *Ibid.* 918–

923. 1952b. [Variety *densa* from southern Florida distinguished by presence of grasslike seedling stage.]

———— & ————. Slash pine (*Pinus Elliottii*) including South Florida slash pine. Nomenclature and description. U. S. Dep. Agr. Southeast Forest Exper. Sta. Pap. **36.** ii + 82 pp. 1954. [Thorough morphological comparisons of *P. Elliottii* and its relatives.]

————, S. LITTLE, & W. T. DOOLITTLE. Natural hybrids among pond, loblolly, and pitch pines. U. S. Dep. Agr. Forest Serv. Res. Pap. **NE-67.** 22 pp. 1967. [Detailed discussion of morphology and distribution of *P. rigida, P. serotina, P. Taeda,* and their hybrids.]

———— & F. I. RIGHTER. Botanical description of forty artificial pine hybrids. U. S. Dep. Agr. Forest Serv. Tech. Bull. **1345.** iii + 47 pp. 1965. [Excellent illustrations of cones of F_1 hybrids and parental taxa.]

LOOCK, E. E. M. The pines of Mexico and British Honduras. S. Afr. Dep. Forestry Bull. **35:** 1–244. 1951.*

LOUDON, J. C. Arboretum et fructicetum Brittanicum. London. 1838. [*Pinus,* **4:** 2152–2292; an important early classification of the genus.]

MARTÍNEZ, M. Los pinos mexicanos. ed. 2. 368 pp. Mexico City. 1948.

MASTERS, M. T. A general view of the genus *Pinus.* Bot. Jour. Linn. Soc. **35:** 560–659. *pls. 20–23.* 1904.

MASTROGIESEPPE, R. J., & J. D. MASTROGIESEPPE. A study of *Pinus Balfouriana* Grev. & Balf. (Pinaceae). Syst. Bot. **5:** 86–104. 1980.

MATTOON, W. R. Life history of the shortleaf pine. U. S. Dep. Agr. Bull. **244:** 1–46. *pls. 1–10.* 1915. [*P. echinata.*]

McCUNE, B. Ecological diversity in North American pines. Am. Jour. Bot. **75:** 353–368. 1988. [Ecological groupings from multivariate comparisons among 34 species.]

McWILLIAM, J. R. The role of the micropyle in the pollination mechanism of *Pinus.* Bot. Gaz. **120:**109–117. 1958.

————. Bioelectric phenomena in relation to pollination in *Pinus.* Silvae Genet. **8:** 59–61. 1959a.

————. Interspecific incompatibility in *Pinus.* Am. Jour. Bot. **46:** 425–433. 1959b.

———— & F. MERGEN. Cytology of fertilization in *Pinus.* Bot. Gaz. **119:** 246–249. 1958.

MERGEN, F. Genetic variation in needle characteristics of slash pine and in some of its hybrids. Silvae Genet. **7:** 1–9. 1958a. [*P. Elliottii.*]

————. Natural polyploidy in slash pine. Forest Sci. **4:** 283–295. 1958b. [Partially polyploid chimeric seedlings found at very low frequency in nursery planting; illustrates their aberrant leaf anatomy and reviews literature on polyploidy in Pinaceae.]

————. Ecotypic variation in *Pinus Strobus* L. Ecology **44:** 716–727. 1963.

————, G. R. STAIRS, & E. B. SNYDER. Natural and controlled loblolly × shortleaf pine hybrids in Mississippi. Forest Sci. **11:** 306–314. 1965.

————, ————, & ————. Microsporogenesis in *Pinus echinata* and *Pinus Taeda.* Silvae Genet. **12:** 128–130. 1966. [Micrographs of meiotic stages; commentary on phenology under conditions of sympatry.]

MILLAR, C. I. The Californian closed cone pines (subsection *Oöcarpae* Little and Critchfield): a taxonomic history and review. Taxon **35:** 657–670. 1986.

————, S. H. STRAUSS, M. T. CONKLE, & R. D. WESTFALL. Allozyme differentiation and biosystematics of the Californian closed-cone pines (subsect. *Oöcarpae*). Syst. Bot. **13:** 351–370. 1988.

MIROV, N. T. The terpenes (in relation to the biology of the genus *Pinus*). Ann. Rev. Biochem. **17:** 521–540. 1948.

————. Taxonomy and chemistry of the white pines. Madroño **12:** 81–89. 1953a.

————. Chemical aspects of *Diploxylon* pines. Silvae Genet. **2:** 93–96. 1953b. [Preliminary comparisons of oleoresin terpenoid and hydrocarbon profiles for the majority of species in the genus.]

———. Photoperiod and flowering of pines. Forest Sci. **2**: 328–332. 1956a.

———. Composition of turpentine of lodgepole × jack pine hybrids. Canad. Jour. Bot. **34**: 443–457. 1956b. [*P. contorta* × *P. Banksiana.*]

———. Distribution of turpentine components among species of the genus *Pinus*. Pp. 251–268 *in* K. V. THIMANN, ed., The physiology of forest trees. New York. 1958.

———. Composition of gum turpentines of pines. U. S. Dep. Agr. Forest Serv. Tech. Bull. **1239**. v + 158 pp. 1961. [Ninety-four species, including all those in our area.]

———. Phenology of tropical pines. Jour. Arnold Arb. **43**: 218, 219. 1962. [Length of reproductive cycle decreased by lack of winter dormancy.]

———. The genus *Pinus*. viii + 602 pp. New York. 1967. [Chapters on paleobotany, geography, morphology, physiology and ecology, chemistry, taxonomy; 105 species recognized.]

———, E. FRANK, & E. ZAVARIN. Chemical composition of *P. Elliottii* var. *Elliottii* turpentine and its possible relation to taxonomy of several pine species. Phytochemistry **4**: 563–568. 1965. [Preliminary investigation of terpenoid chemistry indicates greatest similarity to the Caribbean species of subsect. AUSTRALES.]

MOHR, C. Timber pines of the southern United States, together with a discussion of the structure of their wood, by F. Roth. U. S. Dep. Agr. Bull. **13**. 176 pp. *27 pls.* 1897. [*P. echinata, P. Elliottii, P. glabra, P. palustris, P. Taeda*; maps, excellent illustrations, wood anatomy; notes on *P. serotina.*]

MOSS, E. H. Natural pine hybrids in Alberta. Canad. Jour. Res. C. **27**: 218–229. 1949. [*Pinus contorta* × *P. Banksiana.*]

OWENS, J. N., & M. MOLDER. Seed-cone differentiation and sexual reproduction in western white pine (*Pinus monticola*). Canad. Jour. Bot. **55**: 2574–2590. 1977.

———, S. J. SIMPSON, & M. MOLDER. Sexual reproduction of *Pinus contorta*. I. Pollen development, the pollination mechanism and early ovule development. Canad. Jour. Bot. **59**: 1828–1843. 1981.

———, ———, & ———. Sexual reproduction of *Pinus contorta*. II. Post-dormancy ovule, embryo, and seed development. *Ibid.* **60**: 2071–2083. 1982.

PANETSOS, C. P. Natural hybridization between *Pinus halepensis* and *Pinus brutia* in Greece. Silvae Genet. **24**: 163–168. 1975.

PEATTIE, D. C. White pine; once king of the primeval forests from Maine to Minnesota, the noble conifer has exerted a powerful influence in American history. Sci. Am. **178**(6): 48–53. 1948. [*P. Strobus.*]

PEDERICK, L. A. Chromosome relationships between *Pinus* species. Silvae Genet. **19**: 171–180. 1970. [Detailed karyotypic comparison of secondary constriction patterns for nine species.]

PRUS-GLOWACKI, W., J. SZWEYKOWSKI, & R. NOWAK. Serotaxonomical investigation of the European pine species. Silvae Genet. **34**: 162–170. 1985. [Twelve species of subg. PINUS were well separated from two of subg. STROBUS.]

RZEDOWSKI, J., & L. VELA. *Pinus Strobus* var. *chiapensis* en la Sierra Madre del Sur de México. Ciencia **24**: 211–216. 1966.

SAX, K. Meiosis in interspecific pine hybrids. Forest Sci. **6**: 135–138. 1960.

SAYLOR, L. C. A karyotypic analysis of selected species of *Pinus*. Silvae Genet. **10**: 77–84. 1961. [Compares karyotypes of *P. Strobus, P. Taeda, P. palustris, P. virginiana,* and *P. resinosa.*]

———. Karyotype analysis of *Pinus*—group *Lariciones*. *Ibid.* **13**: 165–170. 1964. [Karyotypes characterized for the 19 species of subsect. LARICIONES.]

———. Karyotype analysis of the genus *Pinus*—subgenus *Pinus*. *Ibid.* **21**: 155–163. 1972. [Forty-six species, including all southern yellow pines.]

———. Karyotype analysis of the genus *Pinus*—subgenus *Strobus*. *Ibid.* **32**: 119–124. 1983. [Twenty-two species, including *P. Strobus.*]

——— & R. L. KOENIG. The slash × sand pine hybrid. Silvae Genet. **16**: 134–138.

1967. [*P. Elliottii* × *P. clausa*, an artificial hybrid between subsects. AUSTRALES and CONTORTAE.]

————— & B. W. SMITH. Meiotic irregularity in species and interspecific hybrids of *Pinus*. Am. Jour. Bot. **53:** 453–468. 1966.

SCHILLER, G., M. T. CONKLE, & C. GRUNWALD. Local differentiation among Mediterranean populations of Aleppo pine in their isoenzymes. Silvae Genet. **35:** 11–19. 1986. [*P. halepensis.*]

SEIKEL, M. K., S. S. HALL, L. C. FELDMAN, & R. C. KOPPEN. Chemotaxonomy as an aid in differentiating wood of eastern and western white pine. Am. Jour. Bot. **52:** 1046–1049. 1965. [*P. Strobus* and *P. monticola* are separable by relative concentrations of certain flavanones.]

SHARP, A. J. *Pinus Strobus* south of the United States. Jour. Elisha Mitchell Sci. Soc. **62:** 629, 630. 1946. [Ecology of *P. Strobus* var. *chiapensis.*]

SHAW, G. R. The pines of Mexico. Publ. Arnold Arb. **1.** 29 pp. *22 pls.* 1909.

—————. The genus *Pinus*. *Ibid.* **5.** 96 pp. 1914. [Important monographic treatment of the genus; excellent illustrations of comparative morphology; 39 plates.]

—————. Notes on the genus *Pinus*. Jour. Arnold Arb. **5:** 225–227. 1924.

SITTMANN, K., & H. TYSON. Estimates of inbreeding in *Pinus Banksiana*. Canad. Jour. Bot. **49:** 1241–1245. 1971. [Simple genetic basis for cone serotiny.]

SMOUSE, P. E., & L. C. SAYLOR. Studies of the *Pinus rigida–serotina* complex. I. A study of geographic variation. Ann. Missouri Bot. Gard. **60:** 174–191. 1973a. [Multivariate comparisons of morphology; *P. serotina* treated as a subspecies of *P. rigida.*]

————— & —————. Studies of the *Pinus rigida–serotina* complex. II. Natural hybridization among the *Pinus rigida–serotina* complex, *P. Taeda* and *P. echinata. Ibid.* **60:** 192–203. 1973b.

SNYDER, E. B., R. J. DINUS, & H. J. DERR. Genetics of longleaf pine. U. S. Dep. Agr. Forest Serv. Res. Pap. **WO-33.** 24 pp. 1977. [*P. palustris.*]

————— & J. M. HAMAKER. Needle characteristics of hybrids of some species of southern pine. Silvae Genet. **27:** 184–188. 1978. [Multivariate comparison of characters differentiating parents and hybrids involving *P. echinata, P. Elliottii, P. palustris, P. Taeda.*]

SQUILLACE, A. E. Geographic variation in slash pine. Forest Sci. Monogr. **10:** 1–56. 1966. [Morphological and physiological variation in *P. Elliottii.*]

————— & O. O. WELLS. Geographic variation of monoterpenes in cortical oleoresin of loblolly pine. Silvae Genet. **30:** 127–135. 1981. [Maps of the geographic variation for major terpene components in *P. Taeda.*]

STEAD, J. W. Studies of variation in Central American pines V: a numerical study of variation in the *Pseudostrobus* group. Silvae Genet. **32:** 101–115. 1983.

STEINHOFF, R. J., & J. W. ANDRESEN. Geographic variation in *Pinus flexilis* and *Pinus strobiformis* and its bearing on their taxonomic status. Silvae Genet. **20:** 159–167. 1971.

—————, D. G. JOYCE, & L. FINS. Isozyme variation in *Pinus monticola*. Canad. Jour. Forest Res. **13:** 1122–1131. 1983.

STYLES, B. T., & P. K. KHOSLA. *In:* IOPB chromosome number reports XLVII. Taxon **24:** 143–146. 1975. [Chromosome numbers, all $2n = 24$, for 16 species of *Pinus.*]

THOMSON, R. B. The spur shoot of the pines. Bot. Gaz. **56:** 362–385. *pls. 20–23.* 1914.

TOMLINSON, P. B. The biology of trees native to tropical Florida. ix + 480 pp. Published by the author, Harvard Univ. Printing Office, Allston, Massachusetts. 1980. [Pinaceae, 61–67; *P. Elliottii* var. *densa,* including two full-page illustrations.]

VAN DER BURGH, J. Hölzer der niederrheinischen Braunkohlenformation, 2. Hölzer der Braunkohlengruben "Maria Theresia" zu Herzogenrath, "Zukunft West" zu Eschweiler und "Victor" (Zülpich Mitte) zu Zülpich. Nebst einer systematisch-anatomischen Bearbeitung der Gattung *Pinus* L. Rev. Palaeobot. Palynol. **15:** 73–275. 1973. [An important account of the systematics of *Pinus,* with a revised classification

emphasizing features of wood anatomy; micrographs of many extant and fossil species.]

WAGNER, D. B., G. R. FURNIER, M. A. SAGHAI-MAROOF, S. M. WILLIAMS, B. P. DANCIK, & R. W. ALLARD. Chloroplast DNA polymorphisms in lodgepole and jack pines and their hybrids. Proc. U. S. Natl. Acad. Sci. **84**: 2097–2100. 1987. [*P. contorta, P. Banksiana.*]

WARD, D. B. Contributions to the flora of Florida—2, *Pinus* (Pinaceae). Castanea **28**: 1–10. 1963. [Key, maps, ecological notes; *P. clausa* var. *immuginata* published for the open-coned race of sand pine.]

————. On the scientific name of the longleaf pine. Rhodora **76**: 20–24. 1974. [*P. palustris* Miller, rather than the later names *P. australis* Michx. f. or *P. longifolia* Salisb. See FERNALD for opposite argument.]

WATTS, W. A. Late-Quaternary vegetation history at White Pond on the inner Coastal Plain of South Carolina. Quaternary Res. **13**:187–199. 1980. [Late Pleistocene fossil needles of *P. Banksiana* from the southeastern United States; see also Ecology **51**: 17–33. 1970, which records this species from northwestern Georgia contemporaneous with the main Wisconsin glaciation.]

WELLS, O. O. Geographic variation in ponderosa pine. I. The ecotypes and their distribution. Silvae Genet. **13**: 89–103. 1964. [Five ecogeographic races recognized based on common orchard studies.]

————, W. I. NANCE, & B. A. THIELGES. Variation in needle traits in provenance tests of *Pinus Taeda* and *P. echinata.* Silvae Genet. **26**: 125–130. 1977. [The two species are well separated in discriminant analyses of needle characters despite broadly overlapping geographic ranges.]

WHEELER, N. C., R. P. GURIES, & D. M. O'MALLEY. Biosystematics of the genus *Pinus,* subsection *Contortae.* Biochem. Syst. Ecol. **11**: 333–340. 1983. [Electrophoretic and morphological comparisons of *P. virginiana, P. clausa, P. contorta,* and *P. Banksiana.*]

WRIGHT, J. W. Species hybridization in the white pines. Forest Sci. **5**: 210–222. 1959.

WU, C. L. The taxonomic revision and phytogeographical study of Chinese pines. (In Chinese; English summary.) Acta Phytotax. Sinica **5**: 131–163. *pls. 24–27.* 1956.

YOSHIE, F., & A. SAKAI. Types of Florin rings, distributional patterns of epicuticular wax, and their relationships in the genus *Pinus.* Canad. Jour. Bot. **63**: 2150–2158. 1985. [The subgenera STROBUS and PINUS are largely distinct in the form of their stomatal complexes and their epicuticular wax patterns.]

ZAVARIN, E. Taxonomy of pinyons based on terpenoids from wood oleoresin and on morphological and other biological characters. Proc. 2nd Piñon Symp., Chapingo, Mexico. (In press.) [Reviews systematics of subsect. CEMBROIDES.]

————, W. B. CRITCHFIELD, & K. SNAJBERK. Turpentine composition of *Pinus contorta* × *Pinus Banksiana* hybrids and hybrid derivatives. Canad. Jour. Bot. **47**: 1443–1453. 1969.

———— & K. SNAJBERK. Oleoresins of pinyons. Agr. Food Chem. **28**: 829–834. 1980. [Survey of the terpenoid composition of wood and gum turpentines from eleven taxa.]

———— & ————. Monoterpene differentiation in relation to the morphology of *Pinus culminicola, Pinus Nelsonii, Pinus Pinceana* and *Pinus Maximartinezii.* Biochem. Syst. Ecol. **15**: 307–312. 1987. [Compares wood monoterpenes and morphological features for these unusual Mexican species of subsect. CEMBROIDES.]

————, ————, D. K. BAILEY, & E. C. ROCKWELL. Variability in essential oils and needle resin canals of *Pinus longaeva* from eastern California and western Nevada in relation to other members of subsection *Balfourianae.* Biochem. Syst. Ecol. **10**: 11–20. 1982. [Compares wood and leaf terpenoids of the bristlecone and foxtail pines and the Mexican *P. Rzedowskii,* which is chemically distinct from the species of subsect. BALFOURIANAE.]

ZOBEL, B. The natural hybrid between Coulter and Jeffrey pines. Evolution 34: 405–413. 1951. [*P. Coulteri* × *P. Jeffreyi.*]

2. **Picea** A. Dietrich, Fl. Gegend Berlin, 794. 1824.

Pyramidal evergreen trees (or shrubs under harsh conditions) with slender, more or less whorled branches. Branchlets pubescent with simple trichomes or glabrous, roughened by persistent leaf bases. Bark thin and scaly or sometimes furrowed. Wood with axial and radial resin canals and ray tracheids regularly present; axial parenchyma absent. Leaves spirally arranged, linear, 4-sided and then stomatiferous on all sides [or dorsiventrally flattened and stomatiferous on the lower—but morphologically adaxial—surface], acute to acuminate, often sharply pointed [or sometimes obtuse or emarginate]; fibrovascular bundle apparently single [or often double]; resin canals 2 [rarely 1], laterally placed; leaf bases persistent, ultimately woody. Pollen cones (microsporangiate strobili) subsessile [or stalked], borne singly in axils of leaves of previous year; microsporophylls many per strobilus, each with apex prolonged into a broad, nearly circular crest; microsporangia longitudinally dehiscent; pollen bisaccate. Ovulate cones borne at tips of previous year's growth, maturing in 1 year, before pollination erect on short stalks; mature cones ovoid to cylindrical, 2–7[–15] cm long, sessile or short stalked, pendulous; bracts much smaller than scales at maturity; ovuliferous scales persistent, obovate to oblong, with apex rounded [to rhombic], entire to denticulate [erose]. Seeds with thin terminal wing; body rounded on the sides and usually acute at base; seed coat without resin vesicles. Cotyledons ca. 6 [4–15], denticulate or entire. Chromosome number $2n = 24$. TYPE SPECIES: *Picea rubra* A. Dietr., *nom. illeg.*, = *P. Abies* (L.) Karst.; see Britton, N. Am. Trees, 54. 1908. (Classical Latin name for a conifer, from *pix*, pitch.)—SPRUCE.

A well-defined genus of approximately 35 species, *Picea* occurs widely in the boreal and temperate areas of the Northern Hemisphere, from the arctic of North America and Eurasia south to the higher mountains of Mexico and southern China. The greatest number of species (ca. 24) occurs in eastern and central Asia, where the taxonomic situation is particularly complex (see Cheng & Fu; Rehder, 1940; Schmidt-Vogt, 1977; Wright). Seven species are native to the United States and Canada; three of these occur in the eastern part, with only one, *P. rubens* Sarg., ranging south into our region.

Sections within *Picea* are not easily distinguished on the basis of overall morphology, chemistry, or crossability. Willkomm divided the genus into two sections, *Eupicea* Willk. (= sect. PICEA) and OMORIKA Willk., based on the cross-sectional form and stomatal arrangement of the needles. Mayr divided the genus into three sections, *Morinda* (= sect. PICEA), CASICTA, and OMORIKA, on the basis of cone-scale shape and texture, in addition to the needle characters noted above. A number of later authors (Bobrov, 1970; Dallimore & Jackson; Gaussen, 1966; Krüssmann; Rehder, 1940) have used this three-section classification, but there has been considerable disagreement over the placement of several species (see comparisons in Schmidt-Vogt, 1977). Wright, in a worldwide treatment utilizing both crossability data and comparisons of overall morphological similarity, found no clear-cut groups among the species. Thus

neither his treatment nor the more recent monograph by Schmidt-Vogt (1977) divided the genus into sections. Preliminary comparisons of monoterpene profiles (Schantz & Juvonen; Von Rudloff, 1975), leaf phenolics (Wellendorf & Kaufmann), and electrophoretic alleles (Wellendorf & Simonsen), as well as further crossability data (Fowler; Mikkola, 1969, 1972), also did not yield groups concordant with the earlier morphological sections. Smaller groups of morphologically similar species recognized as series by Bobrov (1970) seem to be of greater utility.

Our only species, *Picea rubens* (*P. australis* Small; *P. rubra* (Du Roi) Link, non *P. rubra* A. Dietr.), red spruce, yellow spruce, he-balsam, $2n = 24$, a prominent forest tree of the cooler parts of northeastern United States and adjacent Canada, occurs from eastern Ontario east to Nova Scotia, south to Pennsylvania, northern New Jersey, and Delaware, and locally south in the Appalachians to the higher mountains of eastern Tennessee and western North Carolina (Little, 1971, *maps 41N, E*). The species occurs most commonly on well-drained, rocky slopes, as compared to the closely related black spruce (*P. mariana* (Miller) BSP.), which is generally found on wet, boggy soils where it overlaps the range of the red spruce in the northeastern United States and southeastern Canada (Gordon, 1976; Manley & Ledig).

Red spruce differs from black spruce in having lustrous dark or bright green (rather than glaucous) leaves and ovoid-cylindrical, reddish brown, ovulate cones that are usually deciduous at maturity (vs. ovoid, dull gray ones that persist for several years). Both red and black spruce have sharply pointed four-sided leaves and pubescent branchlets, and both are unusual in the genus in having terminal buds with awl-shaped points on their outer scales. Monoterpene profiles are also very similar for the two species (Von Rudloff, 1967a, b; Wilkinson & Hanover). Reports of *P. mariana* in the southern Appalachians (e.g., by Small) are erroneous and based on material of *P. rubens*.

Hybridization between red and black spruces is well documented (Gordon, 1976; Manley; Morgenstern & Farrar) in areas where the two come in contact in southern Canada, but the prevalence of intermediate plants is apparently limited by the habitat differences between the species, relatively low crossability between them (Gordon, 1976), and natural selection against hybrids and hybrid derivatives. Manley & Ledig reported a lack of heterosis and found that photosynthetic rates of hybrids and backcrosses were significantly lower than those of the parental species under all environmental regimes examined. Khalil, however, did find heterosis in hybrids from the lowlands of New Brunswick. The significant geographic variation in morphological and physiological characters within *Picea rubens* found in Khalil's long-term provenance studies appears to reflect selection along latitudinal and altitudinal gradients, as well as effects of hybridization and backcrossing.

During late Pleistocene times additional species of *Picea* occurred in the southeastern United States (Watts). Large cones (up to 10 cm long) that appear to represent an undescribed species similar to *P. glauca* (Moench) Voss, white spruce, have been found as fossils at sites in Louisiana, Tennessee, and Georgia (Critchfield; Delcourt & Delcourt).

Picea comprises a natural group, as is indicated by the overall similarity and crossability among its species (Wright), and is appropriately treated as a distinct

genus. It differs from the other pinoid genera primarily in lacking their unusual derived features, as detailed in the family treatment. It also differs from each of these genera in having leaves that are squarish in cross section and with prominent, persistent bases. As noted in the family treatment, *Picea, Cathaya,* and *Pinus* are apparently the only genera in the Pinaceae that produce the unusual serratene triterpenoids (He *et al.*; Hegnauer, 1986). *Pinus* and *Picea* are quite similar in the details of their pollination mechanisms. *Picea* differs from *Pinus* and *Cathaya* in lacking cleavage polyembryony (Doyle & Brennan) and in having a more asymmetric karyotype.

Chromosome numbers have been reported for 22 of the 36 species of *Picea* recognized by Schmidt-Vogt (see particularly Kuo *et al.*; Santamour, 1960; Sax & Sax; Seitz), with all species having $2n = 24$. Aneuploid and polyploid seedlings have been found at very low frequency in nursery plantings of *P. Abies* (Kiellander), but these presumably would not survive in nature. Supernumerary (B) chromosomes have been reported from some populations of *P. sitchensis* (Bong.) Carr., *P. glauca,* and *P. obovata* Ledeb. (*P. Abies* var. *obovata* (Ledeb.) Fellm.) but are lacking in others (Herzog; Moir & Fox; Pravdin *et al.*). Increase in nuclear-DNA content with latitude has been reported for *P. glauca* and *P. sitchensis* by Miksche (1968, 1971), but this has not been confirmed in wider sampling by Teoh & Rees.

Intergradation or more limited hybridization among species is an important factor in the taxonomic complexity seen in *Picea.* Wright proposed that a number of Asian taxa of uncertain status were the variable products of interspecific hybridization. Among the North American species, *P. glauca* and *P. Engelmannii* Parry show an extensive zone of intergradation in western Canada and Montana (Daubenmire; La Roi & Dugle; Ogilvie & Von Rudloff; Roche), leading some authors (e.g., T. M. C. Taylor, 1959) to treat these taxa as ecogeographic subspecies. Relatively frequent hybridization in regions of sympatry is also seen between the more obviously distinct species *P. sitchensis* and *P. glauca* (Daubenmire; Nienstadt & Teich; Roche), as well as *P. rubens* and *P. mariana,* discussed above. In contrast, the widely sympatric *P. glauca* and *P. mariana* only rarely hybridize (Little & Pauley) and are very difficult to cross artificially (Fowler). The closely related *P. Engelmannii* and *P. pungens* Engelm. may hybridize to a limited degree in areas of sympatry in the southern Rocky Mountains, but no evidence for this was seen in the electrophoretic study of Mitton & Andalora.

Extensive programs of artificial interspecific crossing have been undertaken in *Picea* (Bongarten & Hanover; Fowler; Gordon, 1976; Mikkola, 1969, 1972; Wright), resulting in a substantial number of verified hybrid combinations, including several involving species from different continents. The infrageneric groupings proposed by Mikkola (1969) and Fowler on the basis of crossability agree poorly with those based on leaf anatomy. For example, *P. mariana* and *P. rubens* are more readily crossable with the morphologically dissimilar *P. omorika* (Pančić) Purkyne than they are with one another (Gordon, 1976), perhaps because of selection against hybridization in the two partially sympatric species (Fowler). Prezygotic barriers to hybridization (e.g., failure of the pollen tube to penetrate the nucellus) and early postzygotic barriers have been detailed for a number of interspecific combinations by Mikkola (1969).

Detailed expositions of the comparative leaf anatomy of *Picea* are given by Marco and Colleau. Species assigned to sect. OMORIKA have needles dorsiventrally flattened to varying degrees and are unusual in generally having stomata only on the adaxial leaf surface, which faces downward due to twisting of the leaf base. *Picea sitchensis,* however, often has stomata on all four sides of the leaf (Marco). Colleau attempted to limit sect. OMORIKA to those species with a foliar stomatal density greater than 80 per mm², but it is unclear that this yields a more natural group. Resin canals in species of sect. OMORIKA are near the abaxial leaf surface, while those in the other species are usually adjacent to the lateral angles of the leaf. The leaf mesophyll is differentiated into palisade and mesophyll cells in some species with flattened needles and in some with quadrangular ones (Marco). Another interesting feature of the leaves is the variation in color from bluish to greenish in some species—for example, *P. pungens* (Colorado blue spruce)—due to differences in the amount and structure of the surface wax (Hanover & Reicosky).

Leaf-terpenoid patterns in *Picea* have been critically reviewed by Von Rudloff (1975), following the earlier treatment of Schantz & Juvonen. Von Rudloff found relatively minor differences between some of the species assignable to sects. OMORIKA (*P. omorika* and *P. Breweriana* S. Watson) and PICEA (*P. rubens* and *P. mariana*), but greater ones among other species assignable to the latter section or to sect. CASICTA. Schantz & Juvonen also found differences in leaf- and stem-terpenoid composition to be greater within than among the sections of *Picea.* The degree of geographic or intrapopulational variation in leaf-terpene composition is quite limited in some species (e.g., *P. mariana* and *P. rubens;* Von Rudloff, 1975) but quite variable in others (such as *P. Engelmannii*).

Leaf-stilbene spot patterns and their intensities were surveyed for 23 species of *Picea* by Wellendorf & Kaufmann, who found no clear-cut subgroups within the genus. It has been alleged that sect. OMORIKA is distinct in its leaf-stilbene profile, but this has not been substantiated (Hegnauer, 1962, 1986). Overall leaf-phenolic profiles have proved useful in differentiating *Picea* species in the western United States and Mexico (La Roi & Dugle; R. J. Taylor & Patterson).

A number of species of *Picea* are heavily utilized for pulpwood, lumber for construction, and specialized wood products, with *P. Abies* in Europe, and *P. sitchensis* and *P. glauca* in North America, being of particular economic importance. Acid rain has recently had serious effects on spruce forests in central Europe (e.g., the Black Forest in Germany) and is also adversely affecting *P. rubens* populations from northern Vermont southward in the Appalachian Mountains. Wood of *P. Abies* and *P. glauca* has been valued for violins and for the sounding boards of keyboard instruments, while the high strength-to-weight ratio of the wood of *P. sitchensis* made it particularly valuable for aircraft construction (Dallimore & Jackson). Spruces are frequently grown as ornamentals in the cooler parts of the North Temperate Zone, with Norway spruce (*P. Abies*) and Colorado blue spruce (the glaucous form of *P. pungens*) the most widely cultivated in the United States. Spruce beer, prepared from *P. rubens* and *P. mariana* in the United States and *P. Abies* in Europe by boiling the leafy shoots with flavorings and sugar, was used as an antiscorbutic on sea voyages, while spruce chewing gum was obtained from the resin of the former two species before chicle became widely utilized (Dallimore & Jackson; Little,

1980). The purified resin of *P. Abies,* known as Burgundy pitch, has been used in medicinal plasters (Dallimore & Jackson), and the pitch of *P. rubens* was similarly utilized in the United States (Krochmal & Krochmal).

REFERENCES:

Under family references see particularly L. H. BAILEY; BEAN; BOUREAU; BUCHHOLZ, 1920, 1931, 1942; BUTTS & BUCHHOLZ; CAMPO & SIVAK; CAMPO-DUPLAN; CHANG; CHENG & FU; C. R. CHOWDHURY, 1962; K. A. CHOWDHURY; CRITCHFIELD; DALLIMORE & JACKSON; DOYLE, 1945, 1963; DOYLE & BRENNAN; DOYLE & KANE; G. ERDTMAN, 1957, 1965; FERRÉ; FLORIN, 1931, 1963; FLOUS; FOWELLS; GAUSSEN, 1966; GREGUSS, 1955, 1972; HE *et al.*; HEGNAUER, 1962, 1986; HICKEL; HO & SZIKLAI; HUNTLEY & BIRKS; KHOSHOO, 1961, 1962; KONAR & NAGMANI; KROCHMAL & KROCHMAL; KRÜSSMANN; KUO *et al.*; LITTLE, 1971, 1980; MAHESHWARI & SINGH; MEHRA & KHOSHOO; MILLER, 1976, 1977, 1985; NORIN; OWENS & SIMPSON; PHILLIPS; PILGER; REHDER, 1940, 1949; SANTAMOUR, 1960, 1966, 1967; SARGENT; SAX & SAX; SEITZ; SINGH; SIVAK; SMALL; STERLING; TAYLOR; TEOH & REES; UENO; VON RUDLOFF, 1975a; and WATTS.

BOBROV, E. G. Generis *Picea* historia et systematica. (In Russian; nomenclature primarily in Latin and English.) Nov. Syst. Pl. Vasc. 7: 5–40. 1970. [New classification of *Picea,* with nine series recognized under the sections of MAYR.]
———. Die introgressive Hybridisation in der Gattung *Picea* A. Dietr. Symp. Biol. Hung. **12:** 141–148. 1972.*
BONGARTEN, B. C., & J. W. HANOVER. Hybridization among white, red, blue, and white × blue spruces. Forest Sci. **28:** 129–134. 1982. [Artificial crosses and backcrosses, with verification based on morphology and terpenoid composition.]
BROOKS, J. E., J. H. BORDEN, H. D. PIERCE, JR., & G. R. LISTER. Seasonal variation in foliar and bud monoterpenes in Sitka spruce. Canad. Jour. Bot. **65:** 1249–1252. 1987.
BULARD, C. Quatre épicéas de la Chine centrale: *P. ascendens, P. brachytyla, P. complanata, P. Sargentiana.* Bull. Soc. Hist. Nat. Toulouse **82:** 177–186. 1947. [Reprinted in Trav. Lab. Forest. Toulouse, Tome I, Vol. IV, Art. XX: 1–10. 1947.]
BURLEY, J. Karyotype analysis of Sitka spruce, *Picea sitchensis* (Bong.) Carr. Silvae Genet. **14:** 127–132. 1965.
COLLEAU, C. Anatomie comparée des feuilles de *Picea.* Cellule **67:** 185–253. *pls. 1–3.* 1968. [Twenty-seven species; keys, descriptions, photomicrographs.]
DAUBENMIRE, R. Taxonomic and ecologic relationships between *Picea glauca* and *Picea Engelmannii.* Canad. Jour. Bot. **52:** 1545–1560. 1974. [Extensive intergradation occurs where the two species meet in the northern Rocky Mountains.]
DELCOURT, P. A., & H. R. DELCOURT. The Tunica Hills, Louisiana-Mississippi late glacial locality for spruce and deciduous forest species. Quaternary Res. 7: 218–237. 1977. [Discusses large-coned *Picea* similar to *P. glauca.*]
FOWLER, D. P. The hybrid black × Sitka spruce, implications to phylogeny of the genus *Picea.* Canad. Jour. Forest Res. **13:** 108–115. 1983. [Groupings based on crossability agree poorly with those from leaf anatomy.]
——— & L. ROCHE. Genetics of Engelmann spruce. U. S. Dep. Agr. Forest Serv. Res. Pap. **WO-30.** ii + 13 pp. 1975. [*P. Engelmannii*; map, crossability data.]
GAUSSEN, H., & M. LACASSAGNE. Les épicéas du Kamchatka. Bull. Soc. Hist. Nat. Toulouse **59:** 190–202. 1930.
GORDON, A. G. Ecology of *Picea chihuahuana* Martínez. Ecology **49:** 880–896. 1968.
———. The taxonomy and genetics of *Picea rubens* and its relationship to *Picea mariana.* Canad. Jour. Bot. **54:** 781–813. 1976. [Detailed comparison of Canadian populations indicates limited hybridization in areas of sympatry.]

GUÉDÈS, M., & P. DUPUY. Morphology of the seed-scale complex in *Picea Abies* (L.) Karst. (Pinaceae). Bot. Jour. Linn. Soc. **68:** 127–141. 1974. [Teratological development of the cone scale.]

HANOVER, J. W. Genetics of blue spruce. U. S. Dep. Agr. Forest Serv. Res. Pap. **WO-28.** iii + 12 pp. 1975. [*Picea pungens*; map, scanning electron micrograph of leaf surface, photos of cone variation.]

———— & D. A. REICOSKY. Surface wax deposits on *Picea pungens* and other conifers. Am. Jour. Bot. **58:** 681–687. 1971. [Comparisons of green and glaucous needles by scanning electron microscopy.]

HERZOG, S. Investigations on chromosomes of Siberian spruce (*Picea obovata* Ledeb.). Silvae Genet. **36:** 42–44. 1987. [No B chromosomes found in a sample of 38 trees.]

KHALIL, M. A. K. Genetic variation in red spruce (*Picea rubens* Sarg.). Silvae Genet. **36:** 164–171. 1987. [Summary of results of 20 years of common garden experiments involving numerous provenances; review of literature on the *P. rubens–P. mariana* relationship.]

KIELLANDER, C. L. Polyploidy in *Picea Abies*. Hereditas **36:** 513–516. 1950. [Found in a very low percentage of seedlings.]

KOSSUTH, S. V., & G. H. FECHNER. Incompatibility between *Picea pungens* Engelm. and *Picea Engelmannii* Parry. Forest Sci. **19:** 50–60. 1973. [Strong but not fully complete barriers to crossing seen at stages prior to fertilization; based on results of a single reciprocal cross.]

LACASSAGNE, M. Étude morphologique, anatomique et systématique du genre *Picea*. Trav. Lab. Forest. Toulouse, Tome II, Sect. VII, Vol. III, Art. I: 1–292. 1934. [Forty-three species described and illustrated; several now placed in synonymy.]

LA ROI, G. H., & J. R. DUGLE. A systematic and genecological study of *Picea glauca* and *P. Engelmannii*, using paper chromatograms of needle extracts. Canad. Jour. Bot. **46:** 649–687. 1968. [Comparison of phenolic profiles indicates substantial intergradation in western Canada.]

LINDQUIST, B. 1948. The main varieties of *Picea Abies* (L.) Karst. in Europe, with a contribution to the theory of a forest vegetation in Scandinavia during the last Pleistocene glaciation. Acti Horti Berg. **14:** 249–342. 1948. [See also MOE.]

LITTLE, E. L., JR., & S. S. PAULEY. A natural hybrid between black and white spruce in Minnesota. Am. Midl. Nat. **60:** 202–211. 1958. [Partially fertile hybrid between the widely sympatric *P. glauca* and *P. mariana* reported for the first time; detailed morphological comparisons of the species.]

MANLEY, S. A. M. The occurrence of hybrid swarms of red and black spruces in central New Brunswick. Canad. Jour. Forest Res. **2:** 381–391. 1972.

———— & F. T. LEDIG. Photosynthesis in black and red spruce and their hybrid derivatives: ecological isolation and hybrid adaptive inferiority. Canad. Jour. Bot. **57:** 305–314. 1979.

MANNERS, G. E., & E. P. SWAN. Stilbenes in the bark of five Canadian *Picea* species. Phytochemistry **10:** 607–610. 1971.

MARCO, H. F. The anatomy of spruce needles. Jour. Agr. Res. **58:** 357–368. *pls. 1–7.* 1939.

MAYR, H. Monographie der Abietineen des Japanischen Reiches. viii + 104 pp. *7 pls.* Munich. 1890. [Divides *Picea* into three sections: *Morinda* Mayr (= sect. PICEA), CASICTA Mayr, and OMORIKA Willk.; also treats *Abies, Tsuga, Larix,* and *Pinus* for Japan.]

MERGEN, F., J. BURLEY, & G. M. FURNIVAL. Embryo and seed development in *Picea glauca* (Moench) Voss after self-, cross-, and wind-pollination. Silvae Genet. **14:** 188–194. 1965.

MIKKOLA, L. Observations on interspecific sterility in *Picea*. Ann. Bot. Fenn. **6:** 285–339. 1969. [Causes of failed seed set in artificial crosses; compares relationships based on morphology and crossability.]

————. Crossability between *Picea Omorika* (Pančič) Purkyne and *P. glauca* (Moench) Voss. *Ibid.* **9:** 33–36. 1972.

MIKSCHE, J. P. Quantitative study of intraspecific variation of DNA per cell in *Picea glauca* and *Pinus Banksiana.* Canad. Jour. Genet. Cytol. **10:** 590–600. 1968.

————. Intraspecific variation of DNA per cell between *Picea sitchensis* (Bong.) Carr. provenances. Chromosoma **32:** 343–352. 1971. [DNA content increases with latitude in the samples examined.]

MITTON, J. B., & R. ANDALORA. Genetic and morphological relationships between blue spruce, *Picea pungens,* and Engelmann spruce, *Picea Engelmannii,* in the Colorado Front Range. Canad. Jour. Bot. **59:** 2088–2094. 1981. [Electrophoretic comparisons of a polymorphic enzyme system provided no evidence of hybridization; multivariate comparisons of morphological characters fail to give complete separation, however.]

MOE, D. The post-glacial immigration of *Picea Abies* into Fennoscandia. Bot. Not. **123:** 61–66. 1970.

MOIR, R. B., & D. P. FOX. Supernumerary chromosome distribution in provenances of *Picea sitchensis* (Bong.) Carr. Silvae Genet. **26:** 26–33. 1977. [B chromosomes occur in varying frequencies in the populations below 53°N lat.; similar B chromosomes also seen in *P. glauca.*]

MORGENSTERN, E. K. Note on chromosome morphology in *Picea rubens* Sarg. and *Picea mariana* (Mill.) B.S.P. Silvae Genet. **11:** 163, 164. 1962.

———— & J. L. FARRAR. Introgressive hybridization in red spruce and black spruce. Univ. Toronto Fac. Forestry Tech. Rep. **4.** 46 pp. 1964.*

NIENSTADT, H., & A. TEICH. Genetics of white spruce. U. S. Dep. Agr. Forest Serv. Res. Pap. **WO-15.** iv + 24 pp. 1971. [*P. glauca*; map, crossability data.]

OGILVIE, R. T., & E. VON RUDLOFF. Chemosystematic studies in the genus *Picea* (Pinaceae). IV. The introgression of white and Engelmann spruce as found along the Bow River. Canad. Jour. Bot. **46:** 901–908. 1968.

OWENS, J. N., & M. D. BLAKE. The pollination mechanism of Sitka spruce (*Picea sitchensis*). Canad. Jour. Bot. **62:** 1136–1148. 1984.

———— & M. MOLDER. Sexual reproduction of white spruce (*Picea glauca*). Canad. Jour. Bot. **57:** 152–169. 1979.

———— & ————. Sexual reproduction of Sitka spruce (*Picea sitchensis*). *Ibid.* **58:** 886–901. 1980.

————, S. J. SIMPSON, & G. E. CARON. The pollination mechanism of Engelmann spruce (*Picea Engelmannii*). Canad. Jour. Bot. **65:** 1439–1450. 1987.

PAGE, C. N., & K. D. RUSHFORTH. *Picea Farreri,* a new temperate conifer from upper Burma. Notes Roy. Bot. Gard. Edinburgh **38:** 129–136. 1980.

PRAVDIN, L. F., G. A. ABATUROVA, & O. P. SHERSHUKOVA. Karyological analysis of European and Siberian spruce and their hybrids in the U.S.S.R. Silvae Genet. **25:** 89–95. 1976. [Similar karyotypes in *P. Abies, P. obovata,* and their hybrids; B chromosomes only in *P. obovata.*]

ROCHE, L. A genecological study of the genus *Picea* in British Columbia. New Phytol. **68:** 505–554. *pl. 1, foldout fig.* 1969.

———— & D. P. FOWLER. Genetics of Sitka spruce. U. S. Dep. Agr. Forest Serv. Res. Pap. **WO-26.** iii + 15 pp. 1975. [*P. sitchensis*; map, crossability data.]

SAFFORD, L. O. *Picea.* Pp. 587–597 *in* Seeds of woody plants in the United States. U. S. Dep. Agr. Agr. Handb. **450.** 1974.

SCHANTZ, M. VON, & S. JUVONEN. Chemotaxonomische Untersuchungen in der Gattung *Picea.* Acta Bot. Fenn. **73:** 1–51. 1966. [Preliminary comparisons of leaf, bark, and wood terpenoids; see discussion in VON RUDLOFF, 1975.]

SCHMIDT-VOGT, H. Die Fichte. Bd. I. Taxonomie. Verbreitung. Morphologie. Ökologie. Waldgesellschaften. xviii + 647 pp. Hamburg. 1977. [Taxonomy and distribution of the species of *Picea* of the world, maps, cone and habit photographs, extensive

bibliography, followed by a monographic treatment of the Norway spruce, *P. Abies,* continued in Bd. II/1. xvi + 563 pp. 1986.]

SINGH, H., & J. N. OWENS. Sexual reproduction of Engelmann spruce (*Picea Engelmannii*). Canad. Jour. Bot. **59:** 793–810. 1981.

SUDO, S. Anatomical studies on the wood of *Picea* with some considerations on their geographical distribution and taxonomy. Bull. Gov. Forest. Exper. Sta. Meguro, Tokyo **215:** 39–130. 1968.*

TAYLOR, R. J., & T. F. PATTERSON. Biosystematics of Mexican spruce species and populations. Taxon **29:** 421–469. 1980. [Univariate distributions and discriminant analyses of morphological data; comparisons of phenolic profiles; *P. mexicana* Martínez a variety of *P. Engelmannii; P. chihuahuana* Martínez is distinct.]

————, S. WILLIAMS, & R. DAUBENMIRE. Interspecific relationships and the question of introgressive hybridization between *Picea Engelmannii* and *Picea pungens.* Canad. Jour. Bot. **53:** 2547–2555. 1975. [Multivariate comparisons of morphology show intermediate individuals in both allopatric and sympatric populations; hybridity not clearly demonstrated.]

TAYLOR, T. M. C. The taxonomic relationship between *Picea glauca* (Moench) Voss and *P. Engelmannii* Parry. Madroño **15:** 111–115. 1959. [Treats both as subspecies of *P. glauca.*]

VON RUDLOFF, E. Chemosystematic studies in the genus *Picea* (Pinaceae). I. Introduction. Canad. Jour. Bot. **45:** 891–901. 1967a. [Includes preliminary comparisons of leaf terpenoids in *P. glauca* and *P. mariana.*]

————. Chemosystematic studies in the genus *Picea* (Pinaceae). II. The leaf oil of *Picea glauca* and *P. mariana. Ibid.* **45:** 1703–1714. 1967b.

WELLENDORF, H., & U. KAUFMANN. Thin layer chromatography of fluorescent phenolic compounds in needles: a review of current activities in *Picea.* Pp. 203–226 *in* D. T. SEALS, ed., EEC symposium on forest tree biochemistry. Luxembourg. 1977. [Multivariate comparisons among 23 species give no clear-cut groups; concentrations within spots tend to increase with latitude.]

———— & V. SIMONSEN. A chemotaxonomic study in *Picea* with isozymes in the seed endosperm. A preliminary report. Pp. 182–193 *in* D. RUDIN, ed., Proceedings of the conference on biochemical genetics of forest trees. Umeå, Sweden. 1978. [Preliminary comparisons of 20 species based on presence/absence of alleles in seven enzyme systems; cluster diagram shows only limited agreement with morphological groups.]

WILKINSON, R. C., & J. W. HANOVER. Geographical variation in the monoterpene composition of red spruce. Phytochemistry **11:** 2007–2010. 1972. [*P. rubens.*]

WILLKOMM, H. M. Forstliche Flora von Deutschland, Österreich und der Schweiz. ed. 2. Leipzig. 1887.* [Divides *Picea* into sections based on leaf form.]

WRIGHT, J. W. Species crossability in spruce in relation to distribution and taxonomy. Forest Sci. **1:** 319–349. 1955. [Important paper summarizing morphology and geographic distribution of the species of *Picea,* as well as results of artificial hybridization.]

YEH, F. C., M. A. KHALIL, Y. A. EL-KASSABY, & D. C. TRUST. Allozyme variation in *Picea mariana* from Newfoundland: genetic diversity, population structure, and analysis of differentiation. Canad. Jour. Forest Res. **16:** 713–720. 1986.

3. **Tsuga** (Endlicher) Carrière, Traité Conif. ed. 1. 185. 1855.

Evergreen trees with pendulous leading shoots and branches. Bark usually furrowed and scaly. Wood pale, without normal resin canals; ray tracheids and axial parenchyma regularly present. Leaves spirally arranged (often appearing 2-ranked due to twisting of leaf bases), linear, flattened and bearing 2 whitened

abaxial stomatiferous bands [or quadrangular and bearing stomata above and beneath], narrowing abruptly to a short petiole, abscising at maturity from the ultimately ligneous leaf bases; apex obtuse and often notched, or acute; margin entire or minutely serrulate; fibrovascular bundle double; resin canal single, abaxial to the vascular cylinder. Pollen cones (microsporangiate strobili) small (ca. 1 cm long), subglobose, stalked, borne singly in leaf axils of previous year; microsporophylls prolonged at tip into a short crest or knob; microsporangia subglobose, transversely dehiscent; pollen grains with saccae reduced to a circular "frill" [or bisaccate in sect. HESPEROPEUCE]. Ovulate cones terminal on short branches, maturing the first year; mature ovulate cones relatively small (1–4[–7] cm long), usually pendulous [rarely erect], with cone scales persistent; bracts shorter than scales [to somewhat protrusive in *T. longibracteata*]; ovuliferous scales suborbicular to oblong, entire or minutely lacerate. Seeds with delicate, obliquely oblong terminal wings; seed coat thin, bearing resin vesicles; cotyledons 2–7. Chromosome number $2n = 24$. LECTOTYPE SPECIES: *Tsuga Sieboldii* Carr.;[5] see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **1:** 62. 1913. (Name in Japanese for one of the species.)—HEMLOCK.

A genus of ten or more species of forest trees in the Temperate Zone of eastern and western North America and eastern Asia west to the Himalayas, both at low elevations and in mountain areas up to near timberline. Four well-marked species occur in the United States, including two in our region, and at least six grow in Asia. Over ten species have been described from China (Downie; Flous, 1936b, 1937), of which several are doubtfully distinct and have been placed in synonymy by Cheng & Fu. Thorough study of their patterns of variability is badly needed. Fossils indicate that the genus was more widespread and diverse in the past, having occurred in Europe well into the Tertiary (Florin, 1963; Kirchheimer; Sivak, 1973).

The species of *Tsuga* have generally been divided into two sections: TSUGA (sect. *Eutsuga* Engelm., sect. *Micropeuce* (Spach) Schneider), with pollen saccae reduced to a frill and stomata only on the lower (abaxial) leaf surface, and HESPEROPEUCE Engelm., with bisaccate pollen and less-flattened, amphistomatic leaves. Section HESPEROPEUCE consists of only two extant species, *T. Mertensiana* (Bong.) Carr. in western North America and *T. longibracteata* Cheng in southern China. The latter species, which is unusual in the genus in having the ovulate cones strongly ascending at maturity and the cone-scale bracts exserted, has otherwise been treated in sect. *Heopeuce* Keng & Keng, and in subg. *Paleotsuga* Miki, which was based on fossil material. French workers of the Toulouse school, beginning with Campo-Duplan & Gaussen, have proposed that the two species of sect. HESPEROPEUCE are actually stabilized intergeneric hybrids, as discussed below.

Section TSUGA is represented in our area by two species. *Tsuga canadensis* (L.) Carr. (*T. americana* (Miller) Farw.), Canada hemlock, eastern hemlock,

---

[5]*Abies Araragi* Sieb., Verh. Batav. Genootsch. **12:** 12. 1830 (*Tsuga Araragi* (Sieb.) Koehne), is an earlier name for *T. Sieboldii.* It was published without a usable description, illustration, or type and was only secondarily validated by Siebold & Zuccarini, Fl. Jap. **2:** 15. 1842, under *Abies Tsuga* Sieb. & Zucc. I thus accept the widely used name *T. Sieboldii* Carr. as correct.

hemlock-spruce, $2n = 24$, is a widely distributed species in the northeastern United States and adjacent Canada (Little, 1971, *maps 91N, E*) that occurs west to Wisconsin, eastern Minnesota, eastern Ohio, and southern Indiana. It is widely distributed in the Appalachian region of our area, ranging south to northern Georgia and northwestern Alabama and west to central Tennessee. It occurs in moist valleys and ravines and sometimes on steep, usually north-facing slopes at lower elevations in the northern part of its range, and on moist slopes and streamsides up to 1500 m altitude in our region. Ecogeographic variation in physiological and morphological features is pronounced between northern and southern provenances of the overall range and between north and south of the Tension Zone in Wisconsin (Eickmeier *et al.*; Ruth), although discrete infraspecific taxa have not been proposed on this basis. *Tsuga canadensis* is characterized by distichous, minutely serrulate leaves with rounded apices, pubescent young branchlets, and short-stalked, brownish to grayish ovulate cones with suborbicular scales. It differs from the rather similar western North American *T. heterophylla* (Raf.) Sarg. in having a broader tree crown and narrower, more sharply defined white stomatal bands on the abaxial leaf surface.

Tsuga caroliniana Engelm., Carolina hemlock, crag hemlock, southern hemlock, $2n = 24$, is a much more narrowly distributed species, occurring locally on dry slopes and ridges and along streamsides in the Appalachian Mountains from western Virginia and northeastern Tennessee south to extreme northeastern Georgia and northwestern South Carolina (Little, 1971, *map 94E*), generally at higher elevations than *T. canadensis*. It differs from the latter in having clearly spirally arranged, entire leaves (see FIGURE 3b) and larger (2–3.5 cm long), yellowish, early-deciduous cones with oblong (vs. broadly rounded) scales (see FIGURE 3k, l, r). Although the two species are reported occasionally to occur sympatrically (e.g., in Stokes County, North Carolina, and Roanoke County, Virginia; Coker & Totten; C. E. Wood, pers. comm.), despite differences in habitat preference, they are very distinct morphologically, and hybridization between them has not been reported.

Tsuga is distinguished from all other genera of the Pinaceae by its abruptly petiolate leaves with only a single resin canal abaxial to the vascular tissue. The genus has often been treated as similar to *Picea* because the twigs of both are roughened by the persistent leaf bases, the cones are usually pendulous at maturity, and prominent short-shoots are lacking. The two genera differ, however, in embryogeny and in their pollination mechanisms (Owens & Blake; Owens & Molder), as well as in the characters of root, stem, and seed anatomy that separate *Tsuga* and the other abietoid genera from *Picea* and the other pinoid genera.

Campo-Duplan & Gaussen and subsequent workers of the Toulouse school in France have proposed that *Tsuga Mertensiana* is an intergeneric hybrid of the western North American *T. heterophylla* and *Picea sitchensis* (Bong.) Carr., and that *T. longibracteata* is a hybrid of *Tsuga* and *Keteleeria*. These hypotheses were based primarily on purported intermediacy for a series of morphological characters and irregularities in the bisaccate pollen of the two hemlock species. No case of natural or artificial hybridization has been confirmed for either of
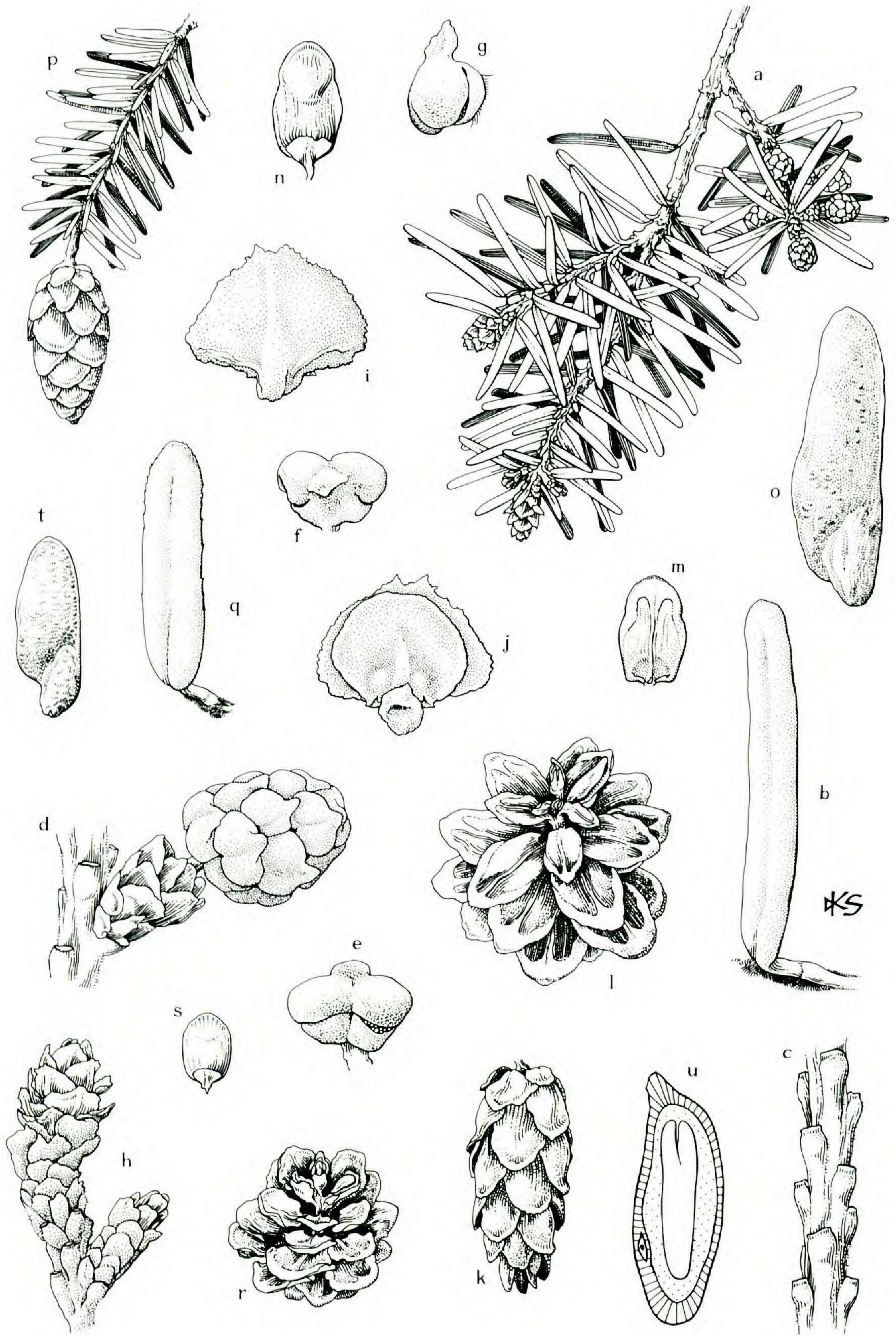
the pairs of genera, however, and it is far more likely that the two taxa involved are merely surviving species that have retained primitive states (e.g., bisaccate pollen) instead of the derived ones seen in sect. TSUGA. Comparison of leaf-terpenoid profiles (Von Rudloff, 1975a, b), immunological distances from seed proteins (Prager *et al.*; Price *et al.*), and patterns of embryological development (Owens & Molder) all show *T. Mertensiana* to be quite similar to other species of *Tsuga* but not to *Picea.*

Chromosome numbers, all $2n = 24$, are known for six species, including all four North American ones (Kuo *et al.*; Sax & Sax; Vabré-Durrieu, 1954b). The karyotype of nine approximately isobrachial and three heterobrachial chromosomes is similar to that of *Picea* (see Khoshoo, 1962; Sax & Sax).

Interspecific hybridization is extremely infrequent among the North American species. *Tsuga × Jeffreyi* (Henry) Henry is a cultivated plant of unknown origin that is morphologically intermediate between *T. Mertensiana* and *T. heterophylla.* Attempts at artificial hybridization between these taxa have been unsuccessful (Meagher; Taylor), but a portion of the infrequent morphological intermediates from areas of near sympatry have proved to be intermediate in leaf-phenolic profile (Taylor).

Comparative pollen morphology of *Tsuga* has been treated in detail by Campo, G. Erdtman (1957, 1965), Sivak, and Ueno (1957). The species of sect. TSUGA are unique in the Pinaceae in having the pollen saccae reduced to a circular frill and in often having spinules atop the verrucate surface ornamentation (G. Erdtman, 1957, 1965; Sivak, 1973). The spinules are apparently absent in *T. canadensis* and are relatively small in *T. caroliniana* and *T. heterophylla* (Sivak, 1973). The size of the two saccae is quite variable within the species of sect. HESPEROPEUCE (Campo; Ho & Sziklai), and fossil *Tsuga* pollen

FIGURE 3. **Tsuga.** a–o, *T. caroliniana*: a, branchlet at time of shedding of pollen, microsporangiate strobili at upper right, 2 ovulate strobili terminating branches below, × 1; b, leaf, showing characteristic entire margin, × 5; c, part of twig after leaf abscission, showing persistent leaf bases, × 6; d, microsporangiate strobilus with bud scales at base, × 6; e–g, microsporophyll with dehisced sporangia, viewed from below, from above, and from side, × 10; h, twig (leaves removed) with terminal ovulate cone (subtended by bud scales), very young leaves beginning to show at tip of short twiglet at right, × 3; i, cone-sale bract (abaxial view) at time of pollination, the smaller ovuliferous scale above completely hidden, × 10; j, adaxial view of ovuliferous scale and bract at time of pollination, micropyles of the 2 ovules below, × 10; k, mature cone in moist condition, cone scales appressed, × 1; l, mature dry cone, seeds already shed, impressions of seed wings conspicuous on ovuliferous scales, × 1; m, n, mature cone scale, adaxial and abaxial views, bract showing at base in n, × 1; o, seed with wing, adaxial view, × 3. p–u, *T. canadensis*: p, branchlet with mature unopened cone (compare leaf arrangement with "a," noting especially the smaller appressed leaves on upper side), × 1; q, leaf, showing serrulate margin and abrupt narrowing to petiole, × 5; r, mature dry cone with seeds shed (compare to "l"), × 1; s, mature cone scale, abaxial view, with bract at base, × 1; t, seed with wing, adaxial view, × 3; u, diagrammatic longitudinal section of seed, with seed coat hatched, megagametophyte stippled, and embryo (with 2 cotyledons) unshaded, × 10.

has been reported to show a wide range of variation between saccate and frilled forms (Kirchheimer; Wodehouse).

In accord with the differences in pollen form, the pollination mechanisms of *Tsuga Mertensiana* and members of sect. TSUGA are quite dissimilar, although both lack the pollination-drop mechanism of *Picea* and *Pinus*. The relatively smooth pollen of *T. Mertensiana* is caught on microdroplets on the integumentary flaps (Owens & Blake). In contrast, the spinulose pollen surface of species such as *T. heterophylla* apparently aids in its adherence to the waxy surface of the bracts, which are much more prominent than the cone scales at this stage of development (Colangelli & Owens; Owens & Blake). Although this unusual pollen-capture mechanism has also been reported in *T. dumosa* (D. Don) Eichler, it needs to be documented in other species of sect. TSUGA (Doyle & O'Leary).

Leaf anatomy of *Tsuga canadensis* has been studied in detail by Gambles & Dengler. Crystals, presumably of calcium oxalate, on the outer surfaces of the leaf-parenchyma cells are an unusual feature to be sought in other species of the genus.

Relatively few comparative chemical studies of *Tsuga* have been made (see Hegnauer, 1962, 1986). Von Rudloff (1975a, b), comparing leaf-terpene profiles of each of the North American species except *T. caroliniana,* found *T. Mertensiana* to be more or less intermediate between *T. heterophylla* and *T. canadensis* and not at all similar to *Picea sitchensis*. Leaf-phenolic pigments of seven species of *Tsuga* were compared by Taylor, yielding a cluster diagram agreeing rather poorly with morphological data. Immunological comparisons of seed-protein extracts (Prager *et al.*; Price *et al.*) indicate that *T. heterophylla* and *T. Mertensiana* are more similar to one another than to representatives of any other pinaceous genus.

Both of our species of *Tsuga* are utilized as ornamentals in the eastern United States, and numerous cultivars of *T. canadensis* have been selected (Den Ouden & Boom; Krüssmann). Bark of *Tsuga* is rich in tannins, and that of *T. canadensis* has been heavily exploited for use in the tanning industry. Wood of most *Tsuga* species is relatively soft and is used most often for crates and paper pulp, while that of *T. heterophylla* is often employed for construction purposes.

REFERENCES:

Under family references see L. H. BAILEY; BEAN; BUTTS & BUCHHOLZ; CARRIÈRE; CHANG; CHENG & FU; C. R. CHOWDHURY (1962); COKER & TOTTEN; DALLIMORE & JACKSON; DEN OUDEN & BOOM; DOYLE, 1945, 1963; DOYLE & KANE; DOYLE & O'LEARY; G. ERDTMAN, 1957, 1965; FERRÉ; FLORIN, 1931, 1963; FLOUS, 1936a; FOWELLS; GAUSSEN, 1966; GREGUSS, 1955, 1972; HEGNAUER, 1962, 1986; HICKEL; HO & SZIKLAI; KHOSHOO, 1961, 1962; KRÜSSMANN; KUO *et al.*; LITTLE, 1971, 1980; MAHESHWARI & SINGH; MILLER, 1976, 1977, 1985; PHILLIPS; PILGER; PRAGER *et al.*; PRICE *et al.*; REHDER, 1940, 1949; SARGENT; SAX & SAX; SINGH; SIVAK, 1975; TAYLOR; UENO; VON RUDLOFF, 1975a; and WODEHOUSE.

BORMANN, F. H., & R. B. PLATT. A disjunct stand of hemlock in the Georgia Piedmont. Ecology **39:** 16–23. 1958. [*T. canadensis.*]

CAMPO, M. VAN. Quelques pollens d'hybrides d'Abiétacées. Silvae Genet. 4: 123–126. 1955. [Illustrates pollen of *T. longibracteata* and *T. Mertensiana* in comparison with that of artificial interspecific hybrids in *Abies*.]

CAMPO-DUPLAN, M. VAN, & H. GAUSSEN. Sur quatre hybrides de genres chez les Abiétinées. Bull. Soc. Hist. Nat. Toulouse 83: 95–109. 1948. [Proposes that *T. longibracteata* and *T. Mertensiana* are actually stabilized intergeneric hybrids; see critiques in DUFFIELD and OWENS & MOLDER.]

CHENG, W.-C. A new *Tsuga* from southwestern China. Contr. Biol. Lab. Sci. Soc. China Bot. 7: 1–3. 1932. [*T. longibracteata*.]

COLANGELLI, A. M., & J. N. OWENS. Pollination mechanism in western hemlock. (Abstract.) West. Forest Genetics Assoc. 1984 Ann. Meeting, 20. 1984. [Pollen adheres preferentially to bracts of the ovulate cone in *T. heterophylla*.]

DOWNIE, D. G. Chinese species of *Tsuga*. Notes Roy. Bot. Gard. Edinburgh 14: 13–19. *pl. 194*. 1923. [Seven species recognized, including five new ones, most of which are now placed in synonymy under *T. yunnanensis* (Franchet) Masters or *T. dumosa* (D. Don) Eichler.]

DUFFIELD, J. W. Review of "Sur quatre hybrides de genres chez les Abiétinées" [VAN CAMPO-DUPLAN & GAUSSEN, 1948]. Jour. Forestry 48: 440. 1950.

EICKMEIER, W., M. ADAMS, & D. LESTER. Two physiological races of *Tsuga canadensis* in Wisconsin. Canad. Jour. Bot. 53: 940–951. 1975. [Physiological and morphological differences between seedlings from northern and southern provenances.]

FITSCHEN, J. Die Gattung *Tsuga*. Mitt. Deutsch. Dendrol. Ges. 1929: 1–12. 1929. [Fifteen species recognized; key; descriptions; habit photographs of six species in cultivation.]

FLOUS, F. Espèces nouvelles du genre *Tsuga*. Bull. Soc. Hist. Nat. Toulouse 69: 409–415. 1936b. [*T. Blaringhemi* (presumably = *T. diversifolia* (Maxim.) Masters), *T. crassifolia* (= *T. Mertensiana* (Bong.) Carr.; isotype, UC!), *T. tchekiangensis* (*T. chinensis* (Franchet) Pritzel var. *tchekiangensis* (Flous) Cheng & L. K. Fu).]

———. Révision du genre *Tsuga*. *Ibid.* 71: 315–450. 1937. [Eighteen species recognized, one a putative hybrid; several are doubtfully distinct.]

GAMBLES, R. L., & N. G. DENGLER. The leaf anatomy of hemlock, *Tsuga canadensis*. Canad. Jour. Bot. 52: 1049–1056. 1974. [Excellent LM and SEM photographs.]

HO, R.-H., & J. N. OWENS. Microstrobilate morphology, microsporogenesis, and pollen formation in western hemlock. Canad. Jour. Forest Res. 4: 509–517. 1974. [*T. heterophylla*.]

JAMES, R. L. Carolina hemlock—wild and cultivated. Castanea 24: 112–134. 1959. [*T. caroliniana*.]

KIRCHHEIMER, F. Über *Tsuga*-Pollen aus dem Tertiär. Planta 22: 171–179. 1934.

MEAGHER, M. D. Studies of variation in hemlock (*Tsuga*) populations and individuals from southern British Columbia. Unpubl. Ph.D. dissertation, Univ. British Columbia, Vancouver. 1976.*

MURRILL, W. A. The development of the archegonia and fertilization in the hemlock spruce (*Tsuga canadensis* Carr.). Ann. Bot. 14: 583–607. *pls. 31, 32*. 1900.

OWENS, J. N., & M. D. BLAKE. Pollen morphology and development of the pollination mechanism in *Tsuga heterophylla* and *T. Mertensiana*. Canad. Jour. Bot. 61: 3041–3048. 1983.

——— & M. MOLDER. Sexual reproduction of mountain hemlock (*Tsuga Mertensiana*). Canad. Jour. Bot. 53: 1811–1826. 1975.

RUTH, R. H. *Tsuga* (Endl.) Carr. Pp. 819–827 *in* Seeds of woody plants in the United States. U. S. Dep. Agr. Agr. Handb. 450. 1974.

SHAW, A. C. The essential oil of *Tsuga canadensis* (L.) Carr. Jour. Am. Chem. Soc. 73: 2859–2861. 1951.

SIVAK, J. Observations nouvelles sur les grains de pollen de *Tsuga*. Pollen Spores 15: 397–457. 1973. [Detailed comparison of pollen from extant and fossil species of sect. TSUGA.]

STANLAKE, E. A., & J. N. OWENS. Female gametophyte and embryo development in western hemlock (*Tsuga heterophylla*). Canad. Jour. Bot. **52:** 885–893. 1974.

UENO, J. Relationships of genus *Tsuga* from pollen morphology. Jour. Inst. Polytech. Osaka Univ. D. **8:** 191–196. *pls. 1, 2.* 1957.

VABRÉ-DURRIEU, A. L'hybride *Tsugo-Picea Hookeriana* et ses parents. Étude des plantules. Bull. Soc. Nat. Hist. Toulouse **89:** 47–54. 1954a. [The purported hybrid *T. Mertensiana* (Bong.) Carr. is more or less intermediate between *T. heterophylla* and *Picea sitchensis* in seedling morphology.]

————. L'hybride *Tsugo-Picea Hookeriana* et ses parents. Étude chromosomique et caryologique. *Ibid.* 401–405. 1954b. [$2n = 24$ for both *Tsuga heterophylla* and *T. Mertensiana.*]

VON RUDLOFF, E. Chemosystematic studies in the genus *Tsuga*. Leaf and twig oil analysis of western hemlock. Canad. Jour. Bot. **53:** 933–939. 1975b. [Terpenoid profiles of *T. heterophylla* differ from those of *T. canadensis* and *T. Mertensiana*; see also VON RUDLOFF (1975a), cited under family references.]

4. **Abies** Miller, Gard. Dict. abr. ed. 4. Vol. 1 (alph. ord.). 1754.

Pyramidal evergreen trees (rarely shrubs at high elevation or latitude) with well-separated "whorls" of branches. Bark with frequent resin blisters, smooth on younger trunks, becoming fissured with age. Wood pale, without normal resin canals (occasionally with traumatic ones); ray tracheids only occasionally present; axial parenchyma present. Leaves spirally arranged (often appearing 2-ranked due to twisting of the leaf bases), linear to linear-lanceolate, flattened and bearing 2 whitened abaxial stomatal bands [less often triangular or quadrangular in cross section and with stomata frequent above, as well as below], obtuse and often notched at apex or acute [to sharply pointed in *Abies bracteata*]; fibrovascular bundle double; resin canals 2 [rarely to 12], in the medial parenchyma [or near the leaf margin]; leaf scars circular, nearly flush with twig [to somewhat raised]. Pollen cones (microsporangiate strobili) short stalked, pendent, borne singly in axils of leaves of previous year; apex of microsporophyll prolonged into a short knob; microsporangia opening transversely; pollen bisaccate. Ovulate cones borne on upper side of topmost branches, maturing the first year; mature cones erect, ovoid [to cylindrical], short stalked or sessile; bracts fimbriate, with apiculate to long-attenuate tips, exserted [or more commonly included]; ovuliferous scales fan shaped, with margin deeply indented near base; bracts and scales abscising from the persistent cone axis. Seeds compressed; body triangular with acute base, the thin terminal wing broadest and often oblique at apex, partially folded over open surface of seed; seed coat thin, with large resin vesicles. Cotyledons [2–]4 or 5[–8 or rarely 14]. Chromosome number $2n = 24$. LECTOTYPE SPECIES: *Abies alba* Miller (*Pinus Picea* L., not *A. Picea* Miller); see Britton, N. Am. Trees, 74. 1908. (Classical Latin name for fir or related conifers.)—FIR, SILVER FIR.

A genus of approximately 40 species, *Abies* is widely distributed in temperate and boreal portions of the Northern Hemisphere, with the largest number of species in mountainous areas. The centers of distribution are in eastern and central Asia (ca. 17 species), southern Europe and North Africa (ca. eight), the western United States and Canada (eight), and Mexico and Guatemala (ca. six). *Abies sibirica* Ledeb. ranges north of the Arctic Circle in the U.S.S.R.,

while *A. lasiocarpa* (Hooker) Nutt. and *A. balsamea* (L.) Miller extend well into the subarctic of North America. *Abies balsamea* and *A. Fraseri* (Pursh) Poiret occur in eastern North America, but only the latter is native to our region.

Infrageneric groups in *Abies* are based on a limited number of morphological characters, which are probably subject to considerable homoplasy, and thus a number of conflicting classifications have been proposed (see comparisons in Critchfield, 1988; Liu). Liu's recent monographic treatment, which is followed here, recognizes two subgenera, PSEUDOTORREYA (Hickel) Franco (including only the unusual California endemic *A. bracteata* D. Don) and ABIES, continuing the precedent of Franco (1942, 1950). Within subg. ABIES, Liu recognized 14 sections based on ovulate-cone, leaf, and branchlet characters. Each of these sections is quite restricted in geographic range, usually to part of a continent. Franco (1950) divided subg. ABIES into seven sections and seven series, with the 11 terminal taxa very similar in composition to those of Liu. The North and Central American species of subg. ABIES fall into three sections (one including two series) in Franco's classification and five in Liu's. The less-formal classification of Gaussen, in which the genus is divided into five sections (one for *A. bracteata* only) and 14 species groups, differs in having sections that include both American and Eurasian species. A significantly different classification by Matzenko (1964, 1968) split the genus into four sections and 18 series based largely on relative size and form of the bracts and scales in the ovulate cone. This treatment often agrees poorly with the preponderance of morphological data and utilizes names without regard to nomenclatural priority. The terminal groups recognized by Liu, Franco, and Gaussen for the North American taxa have proved useful in predicting additional character states such as crossability and distribution of wood crystals. The sectional classifications of the entire genus seem to be fairly arbitrary, however, and should be evaluated using further data on crossability and biochemistry.

Subgenus ABIES is characterized by emarginate to acute (vs. acuminate and callose-tipped) leaf apices, ovate to globose (vs. fusiform) winter buds, and included or exserted bracts without a long-aristate middle lobe. Section BALSAMEAE Engelm. *emend.* Liu (leaves with median resin canals; fibrovascular bundles distinct; ovulate cones oblong to ovoid) comprises three species of the United States and Canada: *A. balsamea, A. lasiocarpa,* and the sole species in our region, *A. Fraseri* (*A. balsamea* var. *Fraseri* (Pursh) Spach), Fraser fir, southern balsam fir, she-balsam. Fraser fir is restricted to higher elevations (ca. 1200–2040 m) in the Appalachian Mountains of southwestern Virginia, eastern Tennessee, and western North Carolina. It occurs in pure stands on cool, moist slopes above 1500 m altitude on Mount Rogers, Roan Mountain, Grandfather Mountain, Mount Mitchell, and Clingman's Dome, and in mixed stands with red spruce (*Picea rubens*) and various hardwoods at lower elevations (Coker & Totten; Liu). In recent years several populations of *A. Fraseri* (e.g., on Mount Mitchell) have declined significantly in size, possibly as a result of the effects of acid rain.

Abies Fraseri is closely related to *A. balsamea,* differing most prominently in having the bracts of the ovulate cone strongly exserted and reflexed (vs.

included or somewhat exserted but not strongly reflexed). *Abies Fraseri* tends to have more lines of stomata per band on the leaves (Fulling, 1934; Rehder, 1940), and its young branchlets pubescent with generally reddish (vs. grayish) hairs. Plants of *A. balsamea* from New England and eastern Canada with somewhat exserted bracts were treated by Fernald as var. *phanerolepis*. Although bract/scale ratio is apparently positively correlated with elevation, it exhibits considerable variation within the northeastern populations (Jacobs *et al.*; Lester, 1968; Myers & Bormann), making this variety not very distinct. Similar plants with a tendency toward exserted bracts are also found scattered in the mountains of West Virginia and northern Virginia in the area between the allopatric ranges of *A. balsamea* and *A. Fraseri*. Several studies (Jacobs *et al.*; Robinson & Thor; Thor & Barnett) have compared these populations to *A. Fraseri* and eastern *A. balsamea* and have found intermediacy but no significant increase in variability in regard to morphological features, terpenoid profiles, or electrophoretic alleles. This is consistent with the hypothesis that these populations are remnants of a previous continuum from which *A. Fraseri* has diverged, rather than products of hybridization. *Abies Fraseri* shows significant differences from *A. balsamea* in the percentage composition of several monoterpenes in the wood and balsam oleoresins (Thor & Barnett; Zavarin & Snajberk, 1972), but only minimal divergence in electrophoretic alleles (Jacobs *et al.*). The two taxa are highly crossable (Hawley & DeHayes, 1985a, b) but are kept distinct by geographic isolation. Given the number of other species in the genus that are subject to partial intergradation, *A. Fraseri* is treated here as a separate species, albeit presumably a recent derivative of *A. balsamea*.

Abies is a distinct genus characterized by a unique combination of characters that separate it from the other abietoid genera of Pinaceae. *Cedrus* and *Pseudolarix* differ from *Abies* in their pronounced shoot dimorphism; *Keteleeria* and *Tsuga* differ in their ovulate cones with persistent scales; and *Tsuga* differs in its cones that are terminal and usually pendulous at maturity. *Abies*, *Keteleeria*, and *Pseudolarix* all have cone scales that are strongly indented at the base, with the seed apex extending beyond the cone scale and the seed wing consequently partially folded over the abaxial surface of the seed, a condition most pronounced in *Abies*. *Abies* and *Keteleeria* are also similar in having circular, only slightly raised leaf scars, but *Keteleeria* differs in its clustered pollen cones, along with its persistent cone scales. Immunological comparison of seed proteins indicates that *Abies* is most similar to *Cedrus* and *Keteleeria* (Price *et al.*).

While the genus is a distinct one, species delimitation within *Abies* is often problematic. Intergradation in morphology and chemistry occurs in a number of areas where related species are geographically adjacent. This could be due to incomplete evolutionary differentiation of taxa or to hybridization between distinct ones, and both of these situations probably occur in *Abies* (Critchfield, 1988). In addition to the *A. balsamea–A. Fraseri* complex discussed above, intermediate populations have been documented in other North American species pairs: *A. concolor–A. grandis* in sect. GRANDES Engelm. (Hamrick & Libby; Von Rudloff, 1976; Zavarin *et al.*, 1977a), *A. balsamea–A. lasiocarpa* in sect. BALSAMEAE Engelm. (Hunt & Von Rudloff; Parker *et al.*; Von Rudloff, 1975a), and *A. magnifica–A. procera* in sect. NOBILES Engelm. (Liu). Inter-

mediate populations between related species are also known in Europe—for example, involving *A. alba* and *A. cephalonica* (Mitsopoulos & Panetsos)—and Asia (Jain; Liu). Disagreements persist as to the distinctness of several Chinese taxa (cf. Cheng & Fu; Gaussen, 1964; Liu; Rushforth, 1983, 1984). Studies of morphological and chemical variation in the Chinese firs are badly needed.

Several artificial interspecific hybrids have been reported in *Abies* (Critchfield, 1988; Hawley & DeHayes, 1985a, b; Klaehn & Winieski; Mergen *et al.*), but many of the early reports were not verified using F_1 morphology or chemistry. Critchfield's (1988) recent review indicates that at least for the North American taxa, interspecific hybrids can frequently be produced within the sections of Liu, but seldom between them. None of the crosses of American and exotic species attempted by Critchfield succeeded, except for that of *A. concolor* with Mexican *A. religiosa,* although earlier reports of unverified crosses of American and Eurasian species need further investigation. In some cases failure of crosses due to embryo abortion or pollen-tube inhibition have been documented (Kormutak; Kormutak & Dubovsky).

Chromosome counts (all $2n = 24$) have been obtained for 22 of the 39 species recognized by Liu and for one putative interspecific hybrid (see especially Khoshoo; Mergen & Burley); *Abies Fraseri* apparently has never been counted. Natural polyploidy within species seems to be very rare. Karyotypes have been investigated by several authors (e.g., Mehra & Khoshoo; Mergen & Burley; Sax & Sax). According to Mergen & Burley, who compared six species of diverse taxonomic affinities and analyzed the effects of different chemical treatments, the three chromosomes with the smallest short arm are clearly heterobrachial and the two with the next longest ones are sometimes heterobrachial. This compares to earlier reports of five heterobrachial chromosomes by Mehra & Khoshoo and Sax & Sax. Secondary constrictions were found by Mergen & Burley to be variable in position and number, even within individual trees.

The pollination mechanism of *Abies* entails adherence of the pollen to microdroplets on the funnel-shaped integument tip, followed by slight infolding of the tip (Doyle & Kane; Owens & Molder; Singh & Owens, 1981, 1982). The pollen is then dormant for up to two months before germinating and growing into the nucellus (megasporangium). Syngamy occurs within a week of pollen germination in the North American species studied by Owens and coworkers. Inefficiencies in the pollination mechanism may be a factor in the high frequency of unfilled seeds seen in several species of firs (Franklin; Owens & Molder). Seed crops also tend to vary substantially in size over two- to several-year cycles (Franklin).

Variation in the form of the bracts and their length relative to the scales in the mature ovulate cones is particularly marked among—and sometimes within—species of *Abies* (Liu). The color of young cones at the time of pollination also varies strikingly, ranging from green or yellowish to various shades of purplish, bluish, or reddish among and sometimes within species (Liu; Sturgeon & Mitton).

Features of leaf anatomy, including number and position of resin canals, presence and distribution of hypodermal cells, degree of separation of the fibrovascular bundles, and distribution of stomata, are often useful in separating species of *Abies* (Fulling, 1934; Liu), although care must be taken to assure

sufficient and comparable samples, since there can be considerable intraspecific variability.

Distribution of calcium-oxalate crystals in the ray parenchyma of the wood has been compared among the nine species of *Abies* native to the United States (Kennedy *et al.*). Rhomboid and elongate crystals are both regularly present in wood samples from five of the western species but are sparse or absent in the western *A. amabilis* (Douglas) Forbes and in the three species of sect. BALSAMEAE (except for elongate crystals in some samples of *A. lasiocarpa*). Rhomboid or elongate crystals have also been reported from the wood of several Asian species (Greguss, 1955, 1972).

Terpenoid profiles from leaf, wood, or bark oleoresins have been used in a number of systematic comparisons among or within species of *Abies* (e.g., Von Rudloff, 1976; Von Rudloff & Hunt; Zavarin & Snajberk, 1965, 1972; Zavarin *et al.*, 1973, 1977a, b, 1978), with emphasis on the North American taxa (see reviews by Critchfield, 1984; Giannasi & Crawford; Von Rudloff, 1975a). These studies have been particularly useful in assessing intergradation among species and in highlighting geographic races within such widespread species as *A. concolor*, *A. balsamea*, and *A. lasiocarpa*. A survey of cortical terpenoids in the Japanese and Taiwanese firs (Zavarin *et al.*, 1978) yielded a diversity of monoterpenoid and sesquiterpenoid compounds and showed partial agreement with previous morphological classifications.

A particularly interesting sesquiterpenoid derivative isolated from the wood of *Abies balsamea* is juvabione, the "paper factor," which exhibits juvenile hormone activity in certain hemipteran insects (Williams). Juvabione and related todomatuic-acid derivatives with juvenile hormone activity have been found in several other *Abies* species and appear to be produced in response to woolly-aphid attack in some (Puritch & Nijholt). This group of compounds has also recently been found in the wood of *Cedrus Deodara* (see Hegnauer, 1986), which is of interest in light of the morphological similarities between these genera. Himachalene sesquiterpenoids characteristic of *Cedrus* have also been found in *Abies* (Zavarin *et al.*, 1978).

Several species of *Abies* are important as ornamental trees, particularly in cool-temperate areas. *Abies balsamea* and others, including *A. Fraseri*, are highly sought after as Christmas trees. Several species of *Abies* are important sources of pulpwood, and fir wood is used for a variety of purposes not requiring great durability. "Canada balsam," employed as a mounting medium in microscopy and as an optical cement, is an oleoresin obtained from the bark blisters of *A. balsamea*, while "Strasbourg turpentine," used in varnishes and artists' paints, is a refined oleoresin from *Abies alba*. Bark and leaf oleoresins from *Abies* have also been utilized medicinally by native peoples in North America to treat colds and to aid wound healing, among other purposes (Arnason *et al.*; Krochmal & Krochmal).

REFERENCES:

Under family references see ARNASON *et al.*; L. H. BAILEY; BEAN; BOUREAU; BUCHHOLZ, 1920, 1931, 1942; BUTTS & BUCHHOLZ; CAMPO & SIVAK; CAMPO-DUPLAN; CHANG; CHENG & FU; C. R. CHOWDHURY, 1962; K. A. CHOWDHURY; COKER & TOTTEN; CRITCHFIELD,

1984; DALLIMORE & JACKSON; DOYLE, 1945, 1963; DOYLE & KANE; G. ERDTMAN, 1957, 1965; FERRÉ; FLORIN, 1931, 1963; FLOUS; GAUSSEN, 1964; GIANNASI & CRAWFORD; GREGUSS, 1955, 1972; HEGNAUER, 1962, 1986; HICKEL; HUNTLEY & BIRKS; KHOSHOO, 1961; KONAR & NAGMANI; KROCHMAL & KROCHMAL; KRÜSSMANN; LITTLE, 1971, 1980; MAHESHWARI & SINGH; MEHRA & KHOSHOO; MILLER, 1976, 1977, 1985; NORIN; OWENS & SIMPSON; PHILLIPS; PILGER; PILGER & MELCHIOR; PRICE *et al.*, 1987; REHDER, 1940, 1949; SARGENT; SAX & SAX; SIVAK; TIEGHEM; UENO; VON RUDLOFF, 1975a; and WATTS.

BOIVIN, B. *Abies balsamea* (Linné) Miller et ses variations. Nat. Canad. **86**: 219–223. 1959. [Suggests that *A. lasiocarpa* be included as a subspecies.]

CLARKSON, R. B., & D. E. FAIRBROTHERS. A serological and electrophoretic investigation of eastern North American *Abies* (Pinaceae). Taxon **19**: 720–727. 1970. [Comparison of seed proteins of *A. Fraseri* and *A. balsamea* by immunology and disc electrophoresis.]

CRITCHFIELD, W. B. Hybridization of the California firs. Forest Sci. **34**: 139–151. 1988. [Reviews crossability among *Abies* species and compares classifications of the genus.]

DANIELS, J. D. Variation and intergradation in the grand fir–white fir complex. 235 pp. Unpubl. Ph.D. dissertation, Univ. Idaho, Moscow. 1969.* [*A. grandis, A. concolor.*]

DEVORE, J. E. Fraser fir in the Unicoi Mountains. Castanea **37**: 148, 149. 1972. [Range extension to Haw Knob on the North Carolina/Tennessee border.]

ENGELMANN, G. A synopsis of the American firs (*Abies* Link). Trans. Acad. Sci. St. Louis **3**: 593–602. 1878.

FERNALD, M. L. A new variety of *Abies balsamea*. Rhodora **11**: 201–203. 1909. [*Abies balsamea* var. *phanerolepis.*]

FRANCO, J. DO A. Sub-géneros e secçães do género *Abies* Mill. Bol. Soc. Port. Ci. Nat. **13**(Suppl. 2): 163–170. *figs. 1–5.* 1942.

———. Abetos. (In Portuguese.) Anais Inst. Sup. Agron. Lisboa **17**: 1–260. *figs. 1–109.* 1950. [Monographic treatment of *Abies*; keys, illustrations for the 20 species cultivated in Portugal.]

FRANKLIN, J. F. *Abies*. Pp. 168–183 *in* Seeds of woody plants in the United States. U. S. Dep. Agr. Agr. Handb. **450**. 1974.

FULLING, E. H. Identification, by leaf structure, of the species of *Abies* cultivated in the United States. Bull. Torrey Bot. Club **61**: 497–524. *pls. 26–32.* 1934. [Keys and extensive illustrations.]

———. *Abies intermedia*, the Blue Ridge fir, a new species. Castanea **1**: 91–94. 1936. [For plants from Virginia and West Virginia that are intermediate between *A. balsamea* and *A. Fraseri.*]

HAMRICK, J. L., & W. J. LIBBY. Variation and selection in western U. S. montane species I. White fir. Silvae Genet. **21**: 29–36. 1972. [*A. concolor.*]

HAWLEY, G. J., & D. H. DEHAYES. Hybridization among several North American firs. I. Crossability. Canad. Jour. Forest Res. **15**: 42–49. 1985a. [*A. balsamea, A. Fraseri, A. lasiocarpa.*] II. Hybrid verification. *Ibid.* 50–55. 1985b.

HUNT, R. S., & E. VON RUDLOFF. Chemosystematic studies in the genus *Abies*. I. Leaf and twig oil analysis of alpine and balsam firs. Canad. Jour. Bot. **52**: 477–487. 1974. [Significant differences between the terpenoid profiles of *A. lasiocarpa* and of *A. balsamea*, and between eastern and western populations of the latter.]

HUTCHINSON, A. H. The male gametophyte of *Abies*. Bot. Gaz. **57**: 148–153. 1914.

———. Fertilization in *Abies balsamea. Ibid.* **60**: 457–472. 1915.

———. Embryogeny of *Abies. Ibid.* **77**: 280–288. 1924.

JACOBS, B. F., C. R. WERTH, & S. I. GUTTMAN. Genetic relationships in *Abies* (fir) of eastern United States: an electrophoretic study. Canad. Jour. Bot. **62**: 609–616. 1984. [Compares *A. Fraseri* to eastern *A. balsamea.*]

JAIN, K. K. Introgressive hybridization in the West Himalayan silver firs. Silvae Genet. **25**: 107–109. 1976. [*A. spectabilis, A. Pindrow.*]

KENNEDY, R. W., C. S. R. SASTRY, G. M. BARTON, & E. L. ELLIS. Crystals in the wood

of the genus *Abies* indigenous to Canada and the United States. Canad. Jour. Bot. **46:** 1221–1228. *pl. 1.* 1968.

KIM, Y. D. Karyological relationships of the genus *Abies* in Korea. (In Korean.) Jour. Korean Forestry Soc. **62:** 60–67. 1983.*

—— & S. S. KIM. Studies on the morphological and anatomical characteristics of the genus *Abies* in Korea. Jour. Korean Forestry Soc. **62:** 68–75.*

KLAEHN, F. U., & J. A. WINIESKI. Interspecific hybridization in the genus *Abies*. Silvae Genet. **11:** 130–142. 1962. [Results of artificial crosses.]

KORMUTAK, A. Cytological study on crossability of some *Abies* species. Biol. Bratislava **36:** 245–251. 1981.*

—— & J. DUBOVSKY. Embryo inviability in *Abies concolor* var. *Lowiana* × *Abies alba* crossing. Biol. Bratislava **39:** 3–14. 1984.*

LAING, E. V. The genus *Abies* and recognition of species. Scot. Forestry **10:** 20–25. 1956. [Keys to vegetative and reproductive material.]

LAMB, W. H. A conspectus of North American firs (exclusive of Mexico). Proc. Soc. Am. Foresters **9:** 528–538. 1914.

LESTER, D. T. Variation in cone morphology of balsam fir, *Abies balsamea*. Rhodora **70:** 83–94. 1968.

——. Geographic variation in leaf and twig monoterpenes of balsam fir. Canad. Jour. Forest Res. **4:** 55–60. 1974.

LIU, T.-S. A monograph of the genus *Abies*. 608 pp. Taipei. 1971. [Includes detailed illustrations and distribution maps.]

MARTÍNEZ, M. Tres especies nuevas mexicanos del género *Abies*. Anal. Inst. Biol. Méx. **13:** 621–634. 1942. [*A. durangensis, A. mexicana, A. Vejari, figs. 1–10.*]

——. Los *Abies* mexicanos. *Ibid.* **19:** 11–104. 1948.

MATZENKO, A. E. The firs of the Eastern Hemisphere. (In Russian; English summary.) Acad. Sci. USSR, Inst. Bot. V. L. Komarov. Flora et Syst. Pl. Vasc. **13:** 1–103. 1964. [New generic classification emphasizing bract and scale characters; extensive bibliography.]

——. Series novae generis *Abies* Mill. Acad. Sci. USSR, Inst. Bot. V. L. Komarov. Novitates Syst. Pl. Vasc. **1968:** 9–12. 1968. [Diagnoses and species for the sections and series in the classification of MATZENKO (1964).]

MEHRA, P. N. Conifers of the Himalayas with particular reference to the *Abies* and *Juniperus* complexes. Nucleus **19:** 123–139. 1976. [*A. Forestii, A. Pindrow, n = 12.*]

MERGEN, R., & J. BURLEY. *Abies* karyotype analysis. Silvae Genet. **13:** 63–68. 1964. [*A. alba, A. cephalonica, A. ×Borisii-regis, A. lasiocarpa, A. firma, A. procera, A. guatemalensis,* all *n = 12.*]

——, ——, & B. A. SIMPSON. Artificial hybridization in *Abies*. Züchter **34:** 242–251. 1964.*

—— & D. T. LESTER. Microsporogenesis in *Abies*. Silvae Genet. **10:** 146–156. 1961.

MITSOPOULOS, D. J., & C. P. PANETSOS. Origin of variation in fir forests of Greece. Silvae Genet. **36:** 1–15. 1987. [Chemical and morphological comparisons of *A. alba, A. cephalonica,* and putative hybrid derivatives.]

MYERS, O., JR., & F. H. BORMANN. Phenotypic variation in *Abies balsamea* in response to altitudinal and geographic gradients. Ecology **44:** 429–436. 1963.

OWENS, J. N., & M. MOLDER. Sexual reproduction of *Abies amabilis*. Canad. Jour. Bot. **55:** 2653–2667. 1977.

PARKER, W. H., J. MAZE, & G. E. BRADFIELD. Implications of morphological and anatomical variation in *Abies balsamea* and *A. lasiocarpa* from western Canada. Am. Jour. Bot. **68:** 843–854. 1981. [Multivariate and univariate comparisons indicate significant intergradation.]

PURITCH, G. S., & W. W. NIJHOLT. Occurrence of juvabione-related compounds in grand fir and Pacific silver fir infested by balsam woolly aphid. Canad. Jour. Bot. **52:** 585–

587. 1974. [Compounds related to juvabione appear to be produced in response to aphid attack on *A. grandis* and *A. amabilis.*]

RAMSEUR, G. S. A hybrid index for the mid-Appalachian *Abies* (fir or balsam). (Abstract.) ASB Bull. **8:** 31. 1961.

REHDER, A. The firs of Mexico and Guatemala. Jour. Arnold Arb. **20:** 281–287. 1939.

ROBINSON, J. F., & E. THOR. Natural variation in *Abies* of the southern Appalachians. Forest Sci. **15:** 238–244. 1969.

ROLLER, K. J. Resin canal position in the needles of balsam, alpine and Fraser firs. Forest Sci. **12:** 348–355. 1966.

RUSHFORTH, K. D. Notes on Chinese silver firs 3. Notes Roy. Bot. Gard. Edinburgh **43:** 269–275. 1986. [See also *Ibid.* **41:** 333–338. 1983; *Ibid.* 535–540. 1984.]

SINGH, H., & J. N. OWENS. Sexual reproduction in subalpine fir (*Abies lasiocarpa*). Canad. Jour. Bot. **59:** 2650–2666. 1981.

——— & ———. Sexual reproduction in grand fir (*Abies grandis*). *Ibid.* **60:** 2197–2214. 1982.

STURGEON, K. B., & J. B. MITTON. Cone color polymorphism associated with elevation in white fir, *Abies concolor*, in southern Colorado. Am. Jour. Bot. **67:** 1040–1045. 1980.

THOR, E., & P. E. BARNETT. Taxonomy of *Abies* in the southern Appalachians: variation in balsam monoterpenes and wood properties. Forest Sci. **20:** 32–40. 1974.

VIGUIÉ, M.-T., & H. GAUSSEN. Révision du genre *Abies.* Bull. Soc. Hist. Nat. Toulouse **57:** 369–434. 1928; **58:** 245–564. 1929. [Reprinted in Trav. Lab. Forest. Toulouse, Tome II, Art. I: 1–386. 1929.]

VON RUDLOFF, E. Chemosystematic studies in the genus *Abies.* II. Leaf oil analysis of grand fir. Canad. Jour. Bot. **54:** 1926–1931. 1976. [Terpenoid variation in south-central Oregon consistent with introgression involving *A. concolor.*]

——— & R. S. HUNT. Chemosystematic studies in the genus *Abies.* III. Leaf and twig oil analysis of amabilis fir. Canad. Jour. Bot. **55:** 3087–3092. 1977.

WARD, D. S. The first record of the Fraser fir. Castanea **27:** 78, 79. 1962.

WILLIAMS, C. M. Hormonal interactions between plants and insects. Pp. 103–132 *in* E. SONDHEIMER & J. B. SIMEONE, eds., Chemical ecology. New York and London. 1970. [Juvenile hormone activity of "paper factor" from *Abies balsamea.*]

ZAVARIN, E., & K. SNAJBERK. Chemotaxonomy of the genus *Abies.* I. Survey of the terpenes present in *Abies* balsams. Phytochemistry **4:** 141–148. 1965. [Preliminary comparison of 17 species, including *A. balsamea* and *A. Fraseri.*]

——— & ———. Geographical variability of monoterpenes from *Abies balsamea* and *A. Fraseri. Ibid.* **11:** 1407–1421. 1972.

———, ———, & W. B. CRITCHFIELD. Monoterpene variability of *Abies amabilis* cortical oleoresin. Biochem. Syst. Ecol. **1:** 87–93. 1973.

———, ———, & ———. Terpenoid chemotaxonomic studies of *Abies grandis. Ibid.* **5:** 89–93. 1977a.

———, ———, & ———. Relation of cortical monoterpenoid composition of *Abies* to tree age and size. Phytochemistry **16:** 770–772. 1977b.

———, ———, & C.-J. LEE. Chemical relationships between firs of Japan and Taiwan. Biochem. Syst. Ecol. **6:** 177–184. 1978. [Cortical terpenoids of six species.]